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论文

简报

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BACK

A behavioral ecology approach to traffic accidents: Interspecific variation in causes of traffic casualties among birds

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Abstract: Birds and other animals are frequently killed by cars, causing the death of many million individuals per year. Why some species are killed more often than others has never been investigated. In this work hypothesized that risk taking behavior may affect the probability of certain kinds of individuals being killed disproportionately often. Furthermore, behavior of individuals on roads, abundance, habitat preferences, breeding sociality, and health status may all potentially affect the risk of being killed on roads. We used information on the abundance of road kills and the abundance in the surrounding environment of 50 species of birds obtained during regular censuses in 2001−2006 in a rural site in Denmark to test these predictions. The frequency of road kills increased linearly with abundance, while the proportion of individuals sitting on the road or flying low across the road only explained little additional variation in frequency of road casualties. After having accounted for abundance, we found that species with a short flight distance and hence taking greater risks when approached by a potential cause of danger were killed disproportionately often. In addition, solitary species, species with a high prevalence of *Plasmodium* infection, and species with a large bursa of Fabricius for their body size had a high susceptibility to being killed by cars. These findings suggest that a range of different factors indicative of risk-taking behavior, visual acuity and health status cause certain bird species to be susceptible to casualties due to cars.

Key words: Birds; Blood parasites; Flight behavior; Flight distance; Habitat selection; Sociality

鸟类交通致死原因的种间行为差异分析

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摘要：鸟类和其他动物经常死于车撞，每年因车撞而死亡的个体可达数百万只。为什么有的物种比其他物种更易于死于车撞的问题，迄今未研究过。该文推测物种本身所具有的冒险行为可能是这些物种的某些个体更常死于车撞的一个原因。此外，不同物种个体在公路上的行为、个体数量、栖息地偏好、繁殖社会性以及健康状况都可能是影响个体车撞风险的潜在因素。2001—2006 年，对丹麦一个农村地区进行定期统计取样，得到该地区不同种鸟类个体被车撞死事件发生的频率，以及周边环境中 50 种鸟类的个体数量数据，并利用这些数据来检验我们的预测。车撞频率随鸟类个体数量线性增加和位于道路上或者低空飞越道路的个体所占比例增加，这两个因素几乎无法解释鸟类车撞频率差异。在考虑到丰富度这个因素后，发现那些鸟类惊飞距离短、面对潜在危险而更具有冒险性的物种个体更易遭遇车撞而亡。另外，独居的物种、疟原虫感染率高的物种及因体型大而拥有大法氏囊的物种个体死于车撞的频率更高。这些发现表明，一系列反映冒险行为、视敏度和健康状况的因子导致某些鸟类物种易受到车撞影响。

关键词：鸟类；血液寄生虫；惊飞行为；惊飞距离；栖息地选择；社会性
中图分类号：Q958.11；Q959.7 **文献标志码：**A **文章编号：**0254-5853-(2011)02-0115-13

The impact of humans on animals has intensified dramatically during the last decades due to increasing human populations and the resulting exploitation of natural resources across the globe (Marzluff et al, 2001).

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Urbanization has a number of consequences for wild animals because of the longer growing season associated with altered micro-climatic conditions, a change in abundance of habitats, an increase in food abundance and hence population density of specific animals, and proximity of humans that may be problematic for species with low thresholds of fear (Batten, 1973; Klausnitzer, 1989; Gliwicz et al, 1994; Stephan, 1999; Shochat et al, 2006; Møller, 2008a). A major impact of urbanization is the construction of roads that disrupt animal movement, but also affect everyday life of animals due to the presence of cars and their effects. For example, recent research has shown strong effects of noise from traffic on song learning and change in composition and carrier frequency of songs (e. g. Reindt, 2003; Warren et al, 2006). Second, roads can have dramatic effects on the distribution of animals (Reijnen & Foppen, 1991; Underhill & Angold, 2000; Forman & Alexander, 1998). A third consequence is the large number of traffic kills due to cars (Blümel & Blümel, 1980; Bruun-Schmidt, 1994; Dunthorn & Errington, 1964; Erritzøe et al, 2003; Finnis, 1960; Göransson et al, 1978; Haas, 1964; Heinrich, 1978; Hodson, 1960; Hodson & Snow, 1965; Nankinov & Todorov, 1983; Smettan, 1988; Straube, 1988; Vignes, 1984; Wäscher et al, 1988). For example, the total number of birds killed by traffic in Denmark alone (a small country of only 43,000 km^2) was estimated to be 3.50 million in the 1960's and 3.27 million in 1980 (Hansen, 1969, 1982). Therefore, the global estimates must at least be hundreds of millions per year.

While the effect of cars on avian mortality is well described, there is to the best of our knowledge no information about the causes of interspecific variation in such mortality. Superficially, one might assume that all species are equally susceptible to traffic mortality because the recent invention of cars has not allowed adaptation to this cause of mortality. However, there might be behavioral or physiological traits that predispose particular species to elevated risk of mortality. Are road-kills just reflecting a random sample of all species according to their abundance and the probability that individuals sit on the road or fly close to the ground, thereby exposing them to traffic accidents, or do specific characteristics of certain species render them more susceptible to being killed by cars? The objectives of this study were to address to which extent the abundance of road-kills of different species could be explained by ecological factors. To this end we estimated both the frequency of road-kills of different species, but also their expected frequency based on standardized birds censuses.

The aims of this study were to assess risk factors associated with road-kills of birds. As a null hypothesis we assessed the importance of abundance as a predictor of the frequency of road-kills of different species, because abundant species by necessity are more likely to end up being killed by cars. Next, we calculated an index of susceptibility to mortality due to cars by quantifying residual variation for each species. First, we hypothesized that species living in open habitats would have a better ability to escape an approaching car because of a better view of the approaching vehicle. Second, Blumstein (2006) has in a study of the evolutionary ecology of fear suggested that flight initiation distance when approached by humans provides a reliable metric of wariness. Flight distance to an approaching human can be considered a metric of the risk that individuals of a given species are willing to take when encountering a potential predator (Blumstein, 2006). Importantly, Møller et al (2008) found that bird species with relatively short flight distances suffered from higher susceptibility to predation by sparrowhawks *Accipiter nisus*, and susceptibility of birds to cat predation is also related to flight distance (Møller et al, 2010). Therefore, species with short flight distances should be particularly susceptible to traffic. Species feeding on fast-moving prey may be better at motion detection (Fleishman et al, 1995) and have more acute visual systems (Garamszegi et al, 2002), making it likely that species eating moving prey would be more flighty than herbivores. Hence, species eating moving prey should be less susceptible to traffic than herbivores. Sociality may involve allocation of more time to monitor conspecifics (Roberts, 1988), making social species more vigilant to an approaching human being (Blumstein, 2006), but incidentally also to approaching cars. Third, we predicted that a relatively short duration of the nestling period for a given body size would imply that fledglings had not fully developed when leaving the nest (Starck & Ricklefs, 1998), resulting in an increased risk of mortality due to cars in such species. Fourth, we predicted that malaria and other blood parasites would affect metabolic efficiency of hosts (Atkinson & Van Riper, 1991; Chen et al, 2001), thereby reducing working ability and hence escape ability when a car is rapidly approaching. Thus, we predicted that bird species with a high prevalence of blood parasites, especially intracellular blood parasites that cause erythrocytes to burst and hence give rise to anemia, would be positively related to susceptibility to car fatalities. Finally, we expected that aspects of immunity in young birds would predict susceptibility to car accidents because such measures of immunity would have evolved in response to parasite-mediated selection, causing species with virulent parasites to have particularly large immune defense organs for their body size. Thus, we predicted a positive relationship between susceptibility to car accidents and relative size of the bursa of Fabricius, which is an important immune defense organ involved in production of antibodies and responsible for differentiation of the repertoire of B-cells in young birds (Glick, 1983, 1994; Toivanen & Toivanen, 1987). Many studies have shown that relative size of the bursa of Fabricius is related to parasite impact on avian hosts (e.g., Garamszegi et al, 2003, 2007; Garamszegi & Møller, 2007; Møller, 2009; Møller & Erritzøe, 1996).

In the present study we were able to assess traffic casualties in relation to null expectations based on abundance and flight behavior. In addition, we performed post mortem autopsies of almost all individuals, verifying that they indeed had died from impact with a car. We tested our predictions concerning risk factors associated with traffic fatalities of birds by relying on an extensive data set of road-kills collected by JE and HE, who also conducted standardized bird censuses in the same sites to quantify the abundance of different species. Therefore, the present study assessed risk factors of traffic mortality in birds, because we could compare observed and expected abundance of road-kills of different species and relate such an index of susceptibility to flight behavior, and ecological and life history characteristics. Thus, we were able to assess the relative importance of a range of different predictors of susceptibility to traffic accidents.

1 Materials and Methods

1.1 Road kills

JE and HE biked or walked 10,500 km on a fixed route during 2001−2006 around Taps (55°27’ N, 9°26’ E), Denmark, with an even distribution of these sampling events throughout the year. The habitat of this open farmland area is open fields, with scattered hedges, plantations and houses with gardens. Traffic is not intense because less than 70 cars were recorded on most censuses. Each trip covered at least 6 km, and they found a total of 461 road-killed birds by carefully searching the road and the verges during these trips. All individuals were aged according to standard criteria reported by Svensson (2006). In addition, all individuals were inspected post mortem, and traffic casualty rather than other causes of mortality was ascertained from severe fractures, blood-filled lungs and other signs of a forceful impact between a bird and a hard obstacle (a car). Thus, we could exclude the possibility that the birds recorded had died for other reasons such as collision with overhead wires, poisoning, predation or other causes of death. The species and their abundance are listed in the Appendix.

JE also recorded all individuals seen during the regular trips, carefully recording whether an individual was sitting on the road or road verge, and whether an individual flew at a height of less or more than 2 m, as judged from our own height. We used this information to estimate the proportion of individuals of each species that was sitting on the road and the proportion of individuals that flew below a height of 2 m as indicators of elevated risk of impact with cars.

A total of 25 of 249 sparrows *Passer* sp. (10%) could not be assigned to species with certainty, and we attributed these unidentified sparrows to house sparrows *Passer domesticus* and tree sparrows *Passer montanus* according to the relative abundance of these two species as road kills of actually identified individuals. However, the results remained unchanged if these 25 unidentified individuals were excluded from the analyses.

1.2 Bird censuses

JE conducted standardized point counts (Bibby et al, 2005) to quantify the abundance of birds during the breeding season and the winter along the roads where road-kills were recorded. In brief, the point counts consisted of 5 minutes being spent per point looking and listening for birds at any distance from the point, while recording these, with 100 m between individual census points, using a total of 20 points per census. Total abundance during the breeding season was estimated as the sum of the seven annual point count censuses made between 2001 and 2006 during the breeding season between 25 May and 1 June. Two winter censuses were conducted on 5 January 2005 and 5 January 2006. We obtained an estimate of total abundance of each species by adding the number of breeding season observations to the number of winter observations multiplied by 3.5, to account for the fact that there were 3.5 times as many breeding season censuses as winter censuses. The bird count results were repeatable among censuses during the breeding season (one-way ANOVA based on the $\log_{10}$-transformed counts: $F = 3.72$, $df = 33{,}170$, $P < 0.0001$) and winter ($F = 4.66$, $df = 7{,}8$, $P = 0.023$), implying that the abundance of different species was consistent among years. The results of these censuses are reported in the Appendix.

1.3 Ecological variables

We scored the main breeding habitats as open grassland (a score of 0), bushes (a score of 1), or trees (a score of 2), relying on information in Cramp & Perrins (1977−1994).

During March-August 2006−2007 APM estimated flight distances for birds in Ile-de-France and Bretagne, France and Northern Jutland, Denmark, using a standard technique developed by Blumstein (2006). Estimates of flight distances are highly consistent among countries, as reported by Møller (2008a, b), hence justifying the use of flight distance data from another population than that used for studying traffic mortality. In brief, when an individual bird had been located while resting, foraging, preening or singing, APM moved at a normal walking speed towards the individual, while recording the number of steps (which approximately equals the number of meters). The distance at which the individual took flight was defined as the flight distance, while in accordance with Blumstein (2006) we defined starting distance as the distance from where the observer started walking until the position of the bird. If the individual was positioned in the vegetation, the height above ground, when APM started walking towards it, was recorded to the nearest meter. While recording these distances, APM also recorded date and time of day, age and the sex of the individual if external characteristics allowed sexing with binoculars. Juveniles were only included when they were fully independent and not fed by adults. Flight distance was estimated as the square-root of the sum of the squared horizontal distance and the squared height (Blumstein, 2006).

All recordings were made during the breeding season, when most individuals are sedentary, thus preventing the same individual from being recorded in different sites, with each site being more than 100 m apart (equaling a territory of 3.1 ha), and for larger species such as herons and corvids APM used a distance of 500 m (equaling a territory of 78.5 ha) because of their larger territories. Using only breeding birds may cause another problem if territorial individuals are less likely to have long flight distances because they are reluctant to cross territory boundaries. However, we can dismiss this alternative explanation because an analysis of 24 species (based on 2018 observations), assessed during winter (December 2006 − February 2007) and summer revealed a strong positive relationship between the two sets of estimates (weighted regression: $F = 41.50$, $df = 1, 3$, $r^2 = 0.64$, $P < 0.0001$).

We assessed the spatial and temporal consistency in estimates of mean flight distances in three ways and found high degrees of consistency (Møller, 2008a,b).

Breeding sociality was quantified as colonial (a score of 1) when individuals used territories that only contained a nest site, and otherwise solitary (a score of 0), using information in Cramp & Perrins (1977−1994).

We extracted information on duration of the incubation and the nestling period from Cramp & Perrins (1977−1994), relying on the value based on the largest sample size if more than a single value was reported. If a range of values was reported, we used the mean of the extreme values. Likewise, we extracted mean body mass from the breeding season from Cramp & Perrins (1977−1994), using the largest sample if more data were reported, and using the mean of means for adult males and adult females, if masses were reported separately for the two sexes.

We used information on prevalence of four genera of blood parasites (*Leucocytozoon*, *Haemoproteus*, *Plasmodium*, *Trypanosoma*), assuming that this would reflect prevalence in the population, as done in previous studies (e. g. Møller & Nielsen, 2007). We also extracted information on the number of individuals examined for each of the host species. In total, the study was based on examination of infection level of 16,995 individual juvenile and adult hosts belonging to 263 species based on blood smears, with a range from 2 to 1539 individuals each for the species [see Møller & Nielsen (2007) for a complete list of sources]. Most of the blood parasite information derived from Northern Europe, where the study of road-kills was also conducted, providing a high degree of overlap between the geographical location of study sites for parasites and car casualties. Scheuerlein & Ricklefs (2004) have shown that prevalence estimates are repeatable across study sites, despite considerable variation among sites and sampling periods. Such variation among sites and sampling periods would make any investigation of relationships between prevalence and ecological variables conservative.

We used information on the mass of the bursa of Fabricius from Møller et al (2005) and Garamszegi et al (2007).

The entire data set is reported in the Appendix.

1.4 Statistical methods

We estimated a susceptibility index to quantify likelihood for individuals of a given species to be killed by traffic, as $\log_{10}$-transformed number of road-kills minus $\log_{10}$-transformed (number of individuals observed of that species divided by the total number of individuals of all species) multiplied by the total number of road-kills). To avoid problems with species having an abundance of road-kills or an overall abundance of zero, we added one to all observations.

Nestling period, mass of bursa of Fabricius, body mass and flight distance were $\log_{10}$-transformed, while the proportion of individuals sitting on the road, the proportion of individuals that flew at a height of less than 2 m and prevalence of blood parasites were square-root arcsine-transformed before analysis.

Most statistical approaches assume that each data point provides equally precise information about the deterministic part of total process variation, i.e. the standard deviation of the error term is constant over all values of the predictor variables (Sokal & Rohlf, 1995). We weighted each observation by sample size (the number of individuals killed by traffic) in order to use all data in an unbiased fashion, thereby giving each datum a weight that reflects its degree of precision due to sampling effort (Draper & Smith, 1981; Neter et al, 1996). Comparative analyses may be confounded by sample size if sampling effort is important, and if sample size varies considerably among taxa. In order to weight regressions by sample size in the analysis of contrasts, we calculated weights for each contrast by calculating the mean sample size for the taxa immediately subtended by that node in the phylogeny (Møller & Nielsen, 2007).

We calculated an estimate of effect size as the Pearson product-moment correlation, using the equations in Rosenthal (1991, pp. 73-74), relying on Cohen's (1988) conventions where $r = 0.1$ equals a small effect, $r = 0.3$ an intermediate effect and $r = 0.5$ equals a large effect).

The three most common species accounted for 75% of all road-kills, implying that these species may have a disproportionate influence on the conclusions. We re-did all analyses after exclusion of these three common species, but all conclusions remained unchanged, suggesting that the three most common species did not bias the findings.

1.5 Comparative analyses

We controlled for similarity in frequency of traffic casualties among species due to common ancestry by calculating standardized independent linear contrasts (Felsenstein, 1985), using the computer program CAIC (Purvis & Rambaut, 1995). Standardization of contrast values was checked by examination of absolute values of standardized contrasts versus their standard deviations (Garland et al, 1992). Plotting the resulting contrasts against the variances of the corresponding nodes revealed that these transformations made the variables suitable for regression analyses. In cases where extreme residuals were recorded, we tested for the robustness of the conclusions by excluding contrasts with studentized residuals greater than 3.00 (Jones & Purvis, 1997). Likewise, we ranked the independent variable to test if the conclusions remained unchanged (Møller & Birkhead, 1994), and in no case did this procedure give rise to conclusions different from those obtained with the contrast values. Ranking provides a very conservative test of a hypothesis, and robustness of findings to ranking of the independent variable thus suggests that distributions of variables are not a confounding factor leading to specific conclusions.

We constructed a composite phylogeny of the 50 species investigated to calculate standardized linear contrasts, mainly based on Sibley & Ahlquist (1990), combined with information from more recent sources (Blondel et al, 1996; Barker et al, 2001, 2004; Crochet et al, 2000; Helbig & Seibold, 1999)(Fig. 1). Because this composite phylogeny was derived from different studies using different phylogenetic methods and different molecular markers, consistent estimates of branch lengths were unavailable. Therefore, we considered branch lengths to be equal in the analyses (this is equivalent to an assumption of a punctuated model of evolution (Purvis & Rambaut, 1995)). We used MacClade to construct the phylogeny and make inferences about the ancestral state of susceptibility to traffic (Maddison & Maddison, 1992).

Regressions of standardized linear contrasts were forced through the origin because the comparative analyses assume that there has been no evolutionary change in a character when the predictor variable has not changed (Purvis & Rambaut, 1995). We used multiple

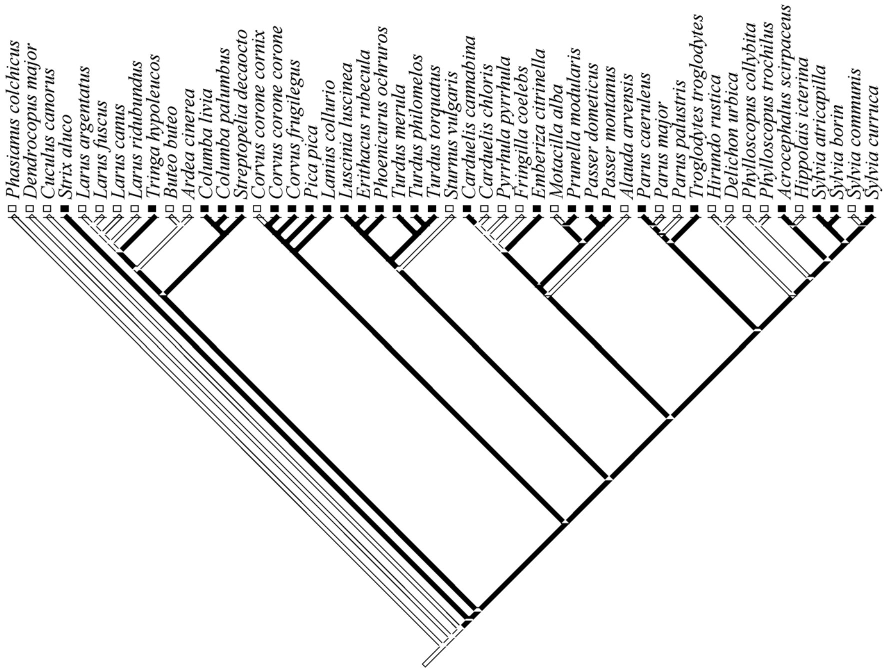

Fig. 1 Phylogeny of species of birds analyzed for road-kills

Species with a relatively low (open branches) and high frequency of road-kills (dark branches), relative to expectations from bird census data, are shown. Hatched branches have equivocal states. See Material and methods for sources.

regression to find the best-fit model, using the software JMP (Anon, 2000). The best-fit model was determined using Akaike's information criterion as an estimate of the improvement in fit for addition of variables (Burnham & Anderson, 2002). There was no evidence of collinearity between variables (Tabacknik & Fidell, 1996).

Information was missing for some species for certain variables, causing sample sizes to differ slightly among analyses.

Values reported are means (*SE*).

2 Results

The number of individuals killed varied among 50 bird species from 0 to 199, with a mean = 9.2, median = 2.0, *SE* = 4.4. The three most abundant species were house sparrow (199 individuals), blackbird *Turdus merula* (95) and tree sparrow (49). The total abundance during censuses of the 50 species varied from 0 to 261 individuals, with a mean = 12.5, median = 2.5, *SE* = 5.4. The frequency of traffic kills increased significantly with abundance in a linear fashion, explaining 42% of the variance (Fig. 2), and the increase was significant both for analyses based on species-specific data and independent contrasts (Tab. 1). The susceptibility index varied from −1.235 to +0.699 with a mean of 0.005 (*SE* = 0.061), not differing significantly from zero (one-sample t-test, t = 0.08, df = 49, P = 0.94). The distribution of the relative frequency of road-kills on the phylogeny showed that the ancestral state among the species studied was a low frequency of traffic casualties (Fig. 1). There were many transitions between different states (Fig. 1), suggesting that ecological factors associated with a relatively high frequency of road-kills were labile.

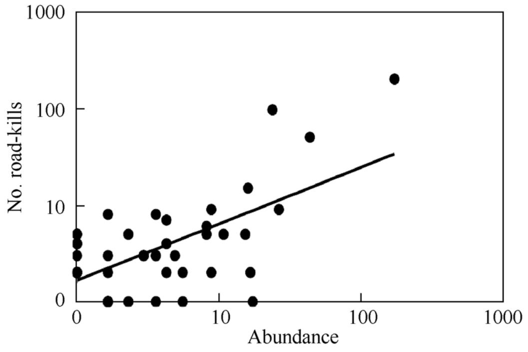

Fig. 2 Frequency of traffic kills in different species in relation to their abundance

The line shows the linear regression line.

The proportion of individuals flying below 2 m ranged from 0 to 1 among species, with a mean value of 0.36 (*SE* = 0.05). The proportion of individuals on the road varied from 0 to 1 among species, with a mean value of 0.31 (*SE* = 0.05). These two variables were not

Tab. 1 Linear regression of log-transformed number of road-kills for different species of birds in relation to log-transformed abundance

Variable	Sum of squares	*df*	*F*	*P*	Slope (SE)	Effect size
Model A (Species):						
log (Abundance)	4.41	1	29.76	< 0.0001	0.513 (0.094)	0.62
Error	7.12	48				
Model B (Contrasts):						
log (Abundance)	0.63	1	18.79	< 0.0001	0.452 (0.104)	0.53
Error	1.61	48				

Model A was based on species-specific data, while model B was based on standardized linear contrasts. Effect size was estimated as the Pearson product moment correlation coefficient.

significantly correlated (Pearson $r = 0.06$, $t = 0.44$, $df = 48$, $P = 0.66$). The proportion of individuals on the road explained a significant amount of variation in road-kills ($F = 6.65$, $df = 1{,}48$, $P = 0.013$, slope (*SE*) = 0.32 (0.12), effect size = 0.35), while that was not the case for the proportion of individuals flying below 2 m ($F = 0.38$, $df = 1{,}48$, $P = 0.54$, slope (*SE*) = 0.08 (0.12), effect size = 0.09). Neither variable explained a significant amount of variation in susceptibility to traffic (proportion of individuals on road: partial $F = 0.81$, $df = 1{,}47$, $P = 0.37$, effect size = 0.13; proportion of individuals flying lower than 2 m: partial $F = 0.07$, $df = 1{,}47$, $P = 0.80$, effect size = 0.04). Flight distance did not significantly predict susceptibility to traffic in a model that included body mass (partial $F = 1.10$, $df = 1{,}42$, $P = 0.30$, effect size = 0.16).

Age did not affect susceptibility to traffic because the proportion of yearlings was not a significant predictor in a model that included body mass as an additional predictor variable (partial $F = 0.14$, $df = 1{,}33$, $P = 0.71$, effect size = 0.06).

Susceptibility to traffic increased from open habitats and bushes to trees in analyses of species-specific data, but not in analyses of contrasts (Tab. 2 models A−B).

Breeding sociality reduced susceptibility to traffic, after inclusion of body mass as an additional predictor variable (Fig. 3A; partial $F = 11.52$, $df = 1{,}46$, $P = 0.0014$, effect size = 0.45). In contrast, food did not significantly predict susceptibility to traffic, after inclusion of body mass as an additional predictor variable (partial $F = 0.00$, $df = 1{,}46$, $P = 0.99$, effect size = 0.01).

Bird species with a long nestling period for their body size were less susceptible to traffic, and this effect was independent of the effect of habitat in analyses of species-specific data and contrasts (Tab. 2 Models A−B). In contrast, the duration of the incubation period was not a significant predictor (results not shown). In addition, susceptibility increased with body mass, although only in analyses of species-specific data (Tab. 2 Models A−B), implying that large species were more susceptible than small species in species-specific analyses.

The prevalence of two genera of blood parasites, *Leucocytozoon* and *Plasmodium*, were both positively related to susceptibility to traffic, with similar effects in analyses of species-specific data and independent contrasts (Tab. 2 Models C-D; Fig. 3B). In contrast, the prevalence of *Haemoproteus* and *Trypanosoma* was not a significant predictor (results not shown for simplicity).

The size of the bursa of Fabricius was positively related to susceptibility to traffic, both in analyses of species-specific data and independent contrasts (Tab. 2 Models E−F; Fig. 3C). This effect was independent of body mass.

Finally, we developed best-fit models that included all the predictor variables. An analysis of species-specific data revealed a model that explained 60% of the variance (Tab. 3 Model A). There were statistically significant effects of flight distance after inclusion of the other variables of interest (Fig. 3D; negative relationship between distance and susceptibility), breeding sociality (solitary species having greater susceptibility than colonial species), and mass of bursa of Fabricius (species with larger bursa being more susceptible) (Tab. 3 Model A). A model based on independent contrasts revealed intermediate to strong effects of flight distance (negative relationship between distance and susceptibility), breeding sociality (solitary species having greater susceptibility than colonial species), food (species eating live prey being less susceptible than herbivores), prevalence of

Tab. 2 Best-fit models of the relationship between susceptibility to mortality due to traffic and (models A-B) habitat, log-transformed nestling period and log-transformed body mass, (models C-D) square-root arcsine-transformed prevalence of *Leucocytozoon* and *Plasmodium* and log-transformed body mass, (models E-F) log-transformed mass of bursa of Fabricius and log-transformed body mass

Variable	Sum of squares	*df*	*F*	*P*	Slope (SE)	Effect size
Model A (Species):						
Habitat	5.35	1	9.14	0.0041	0.12 (0.04)	0.41
Nestling period	6.03	1	10.30	0.0025	−1.20 (0.37)	0.43
Body mass	8.00	1	13.67	0.0006	0.41 (0.11)	0.48
Error	26.33	45				
Model B (Contrasts):						
Habitat	0.76	1	2.01	0.16	0.10 (0.07)	0.20
Nestling period	1.84	1	4.89	0.032	−1.40 (0.63)	0.31
Body mass	0.31	1	0.82	0.37	−0.22 (0.24)	0.13
Error	17.38	46				
Model C (Species):						
Leucocyto-zoon	11.00	1	16.92	0.0002	0.72 (0.18)	0.51
Plasmodium	6.66	1	10.25	0.0025	0.84 (0.26)	0.42
Error	30.55	47				
Model D (Contrasts):						
Leucocyto-zoon	3.22	1	10.27	0.0027	0.84 (0.26)	0.46
Plasmodium	3.85	1	12.25	0.0012	1.27 (0.36)	0.49
Body mass	2.88	1	9.16	0.0044	−0.76 (0.25)	0.44
Error	12.24	39				
Model E (Species):						
Bursa of Fabricius	13.93	1	18.61	< 0.0001	0.41 (0.10)	0.55
Error	32.18	43				
Model F (Contrasts):						
Bursa of Fabricius	1.88	1	4.46	0.041	0.57 (0.27)	0.31
Body mass	2.70	1	6.42	0.015	−0.92 (0.36)	0.36
Error	17.66	42				

Models A, C and E were based on species-specific data, while models B, D, and E were based on statistically independent contrasts. The overall models had the following statistics: Model A: $F = 12.03$, $df = 3,45$, $r^2 = 0.45$, $P < 0.0001$, Model B: $F = 2.82$, $df = 3,46$, $r^2 = 0.15$, $P = 0.049$, Model C: $F = 13.13$, $df = 2,47$, $r^2 = 0.36$, $P < 0.0001$, Model D: $F = 6.13$, $df = 3,39$, $r^2 = 0.32$, $P = 0.0016$, Model E: $F = 18.62$, $df = 1,43$, $r^2 = 0.30$, $P < 0.0001$, and Model F: $F = 3.28$, $df = 2,42$, $r^2 = 0.14$, $P = 0.047$. Effect size was estimated as the Pearson product moment correlation coefficient.

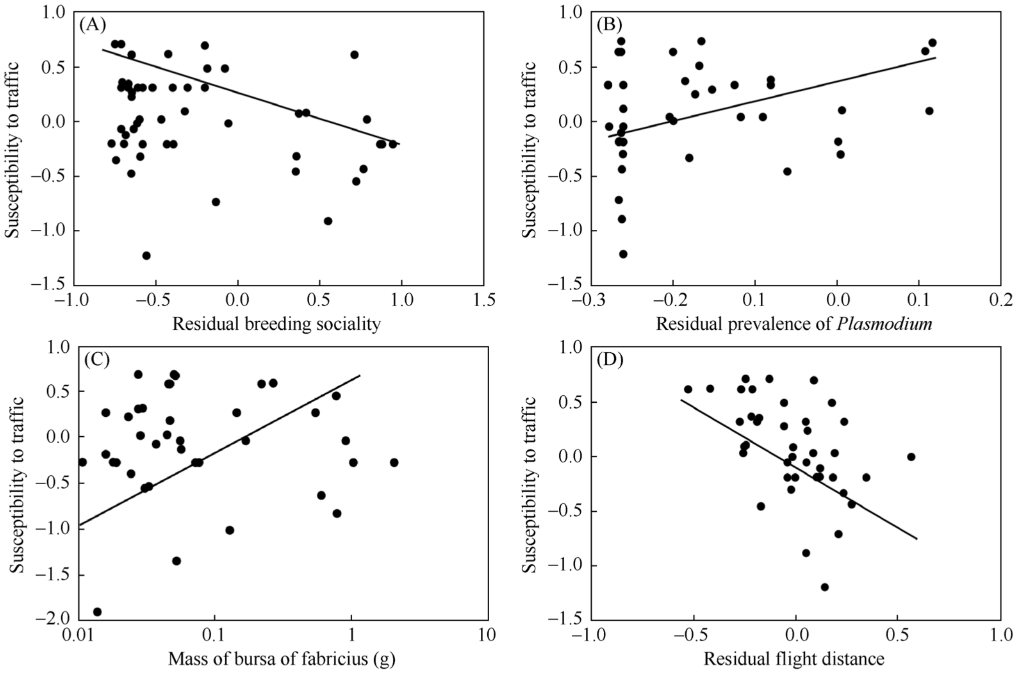

Fig. 3 Susceptibility to traffic death in different species of birds in relation to (A) breeding sociality, (B) relative prevalence of *Plasmodium* (after adjusting for prevalence of *Leucocytozoon* and body mass), (C) mass of the Bursa of Fabricius (g), and (D) flight distance (after adjusting for breeding sociality and mass of bursa of Fabricius)

The lines are the linear regression lines weighted by sample size.

Tab. 3 Best-fit models of the relationship between susceptibility to mortality due to traffic and habitat, log-transformed nestling period, square-root arcsine-transformed prevalence of *Leucocytozoon* and *Plasmodium*, log-transformed mass of bursa of Fabricius and log-transformed body mass

Variable	Sum of squares	*df*	*F*	*P*	Slope (SE)	Effect size
Model A (Species):						
Breeding sociality	9.83	1	19.77	< 0.0001	–0.38 (0.08)	0.59
Flight distance	8.28	1	16.66	0.0002	–0.76 (0.19)	0.56
Bursa of Fabricius	13.90	1	27.96	< 0.0001	0.49 (0.09)	0.66
Error	18.40	37				
Model B （Contrasts）:						
Flight distance	2.50	1	10.43	0.0029	–0.93 (0.29)	0.50
Breeding sociality	3.12	1	13.00	0.0010	–0.52 (0.14)	0.54
Food	1.29	1	5.36	0.027	–0.33 (0.14)	0.38
Plasmodium	2.94	1	12.24	0.0014	1.21 (0.35)	0.53
Bursa of Fabricius	3.42	1	14.25	0.0007	0.89 (0.24)	0.55
Body mass	2.67	1	11.12	0.0022	–1.15 (0.34)	0.51
Error	7.68	32				

Model A was based on species-specific data, while model B was based on statistically independent contrasts. The overall models had the following statistics: Model A: $F = 18.08$, $df = 3{,}37$, $r^2 = 0.59$, $P < 0.0001$, and Model B: $F = 7.57$, $df = 7{,}32$, $r^2 = 0.19$, $P < 0.0001$. Effect size was estimated as the Pearson product moment correlation coefficient.

Plasmodium (species with higher prevalence being more susceptible), bursa of Fabricius (species with larger bursa being more susceptible), and body mass (larger species being less susceptible) (Tab. 3 Model B).

3 Discussion

We provide evidence of avian mortality due to traffic directly reflecting the abundance of different species, but also phenotypic characteristics relating to flight behavior, visual acuity and health status. The null hypothesis investigated was that the abundance of traffic casualties simply reflected the abundance of different species, but also their behavior, with species with many individuals sitting on the road or flying close to the ground experiencing a high risk of mortality due to traffic. Abundance and to a small extent the proportion of individuals that were sitting on the road explained variation in traffic casualties. In addition, risk-taking behavior when approached by a human being estimated in terms of flight distance, breeding sociality (solitary species run higher risks), prevalence of the blood parasites of the genus *Plasmodium* (species with high prevalence run higher risks), and the size of the bursa of Fabricius (species with large immune defense organs run higher risks) all predicted susceptibility to traffic. We will briefly discuss these findings.

Mortality among birds due to traffic may constitute a non-negligible fraction of overall mortality, and Svensson (1998) suggested that this factor is seriously under-estimated. Hansen (1982) estimated that 3.27 million birds died on roads in Denmark in 1980−1981. Given that the total population of birds, including fledglings, consists of 16.29 million pairs (based on the mean estimates reported by Grell (1998)), and assuming that mean clutch size is 4.5 eggs (the mean for 512 species breeding in the Western Palearctic (Cramp & Perrins, 1977−1994), the mean number of clutches per year being 1.6 (the mean for 512 species breeding in the Western Palearctic (Cramp & Perrins, 1977−1994)), and mean nest predation rate being 24% for 72 species (Cramp & Perrins, 1977−1994)), then the total population can be estimated as (16.29 million pairs × 2 individuals per pair) + (16.29 million pairs ×4.5 eggs per clutch × 1.6 clutches per year × 0.76) = 121.72 million individuals. Therefore, mortality due to traffic can be estimated as (3.27 million / 121.72 million), or 2.7%. Given that mean adult mortality rate for 172 bird species from the Western Palearctic (Cramp & Perrins, 1977−1994) was 38%, mortality due to traffic accounted for 2.7% / 38% = 7.1% of overall mortality. This proportion is bound to be an over-estimate because juvenile mortality is likely to be greater than 38%.

However, the conclusion remains that avian mortality due to traffic constitutes a non-negligible fraction of overall mortality in the order of 5%−10% of overall mortality. Whether this has any effect on population size will depend on whether mortality caused by traffic acts in a density-dependent manner. To the best of our knowledge this provides the first estimate of the relative importance of traffic casualties for overall mortality in any group of animals.

The null hypothesis for traffic casualties is that risk of mortality should reflect the abundance of different species and their flight behavior. Abundance explained 42% of the variance in traffic mortality among species. Surprisingly, we found little evidence of flight behavior affecting the abundance of traffic casualties. There was a weak positive relationship between the proportion of individuals of different species being recorded on the road and road-kills, while the proportion of individuals flying at a height of less than 2 m did not predict traffic casualties. This leaves 60% of the variance to be explained by other factors such as sampling effort, ecological factors and other sources of variation.

Blumstein (2006) suggested in his hypothesis about the evolutionary ecology of fear that flight distance should provide a reliable metric reflecting the risk that individuals are willing to take when trading foraging against flight. Studies of flight distance in birds have indicated that urban birds take greater risks than rural conspecifics, as reflected by shorter flight distances (Møller, 2008a). A number of factors hypothesized to provide increased visual acuity such as sociality and reliance on live prey may also allow individuals to escape when approached by a car. We found clear evidence suggesting that flight distance and breeding sociality both predicted susceptibility to traffic, and that was also the case in analyses of contrasts.

Risk of mortality due to traffic was elevated in bird species with high prevalence of blood parasites of the genus *Plasmodium*. While we have no information whether individuals killed by cars were infected by blood parasites, we can conclude that species that had high prevalence of *Plasmodium* suffered disproportionately from traffic mortality. We have no a priori explanation why there were no effects for the blood parasite genera *Haemoproteus* and *Trypanosoma*, although previous studies of blood parasites and predation also showed similar variation among taxa (Møller & Nielsen, 2007). We hypothesize that this effect was due to the impact of malaria as a cause of dramatic increases in the abundance of damaged erythrocytes, thereby severely reducing the efficiency of metabolism, but also restricting blood flow to the brain and the spleen (Atkinson & Van Riper, 1991; Chen et al, 2001). In addition blood parasites cause immune responses, fever and induction of heat-shock proteins (Wakelin, 1996; Merino et al, 1998; Chen et al, 2001), and these effects may affect the ability of an individual to escape when approached by a car. Such effects will be particularly strong for intra-erythrocytic blood parasites like *Plasmodium* that is the cause of severe anemia. Bird species with blood parasite infections have shorter flight distances than uninfected species (Møller, 2008b), suggesting that species with high level infections may take greater risks when encountering potential danger. The increase in mortality risk by traffic linked to blood parasite infections selects against blood parasite infections. The findings reported here also have implications for parasitological studies of blood parasites. Given that traffic-induced mortality disproportionately biases estimates of prevalence of blood parasites downwards, any epidemiological inference based on prevalence in populations of hosts is likely to be biased likewise.

Given the relationship between blood parasite infection and susceptibility to traffic, we should also expect immunity to explain interspecific variation in risk of being killed by a car. Indeed, we found a positive relationship between susceptibility to car accidents and size of the bursa of Fabricius. The bursa is an important immune defense organ involved in production of antibodies and responsible for differentiation of the entire repertoire of B-cells in young birds (Glick, 1983, 1994; Toivanen & Toivanen, 1987). This effect was independent of body mass.

Susceptibility to mortality caused by traffic increased with increasing body mass, when analyzing species-specific data and contrasts. Large bird species need longer distances for take-off, and climb rates decrease with body mass (Hedenström & Alerstam, 1992), and species with large body mass have long flight distances (Møller, 2008a,b). That may partly explain why species with large body mass run a higher risk of mortality due to traffic than small species, although other factors relating to body size may explain this variation. The best-fit model showed a negative relationship with body mass still being present after other predictor variables had been included.

We also investigated susceptibility to traffic in relation to habitat, flight behavior, duration of development and several other factors, but found little evidence of these factors explaining interspecific variation once other factors were included in the phylogenetic analyses.

In conclusion, we have found that risk of mortality in birds due to traffic increased with abundance. Once abundance had been taken into account, solitary species with short flight distances having a high prevalence of malarial parasites and a large bursa of Fabricius were particularly likely to die from traffic accidents. These findings suggest that risk of mortality due to traffic is associated with ability to escape an approaching vehicle. Furthermore, given that mortality due to traffic potentially is a non-negligible cause of mortality in birds the results suggest that car-induced mortality will select for resistance to blood parasites, increased sociality, and longer flight distances.

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Appendix 1 Frequency of road-kills of 50 species of birds, abundance of these species during standard point count censuses, proportion of individuals recorded on the road, proportion of individuals flying below 2 m, duration of nestling period (days), habitat (0 — grassland, 1 — bushes, 2—trees), breeding sociality (0 — solitary, 1 — colonial), mean flight distance (m), body mass (g), prevalence of *Leucocytozoon* and *Plasmodium*, and mass of bursa of Fabricius (g)

Species	Frequency of road-kills	Abun-dance	Proportion of individuals on road	Proportion of individuals flying below 2 m	Nestling period (d)	Ha-bitat	Breeding sociality	Flight distance (m)	Body mass (g)	Prevalence of *Leucocy-tozoon*	Prevalence of *Plasmodium*	Mass of bursa of Fabricius (g)
Acrocephalus scirpaceus	1	0	0.00	1.00	10.9	0	0	6.73	11.80	0.01	0.02	0.016
Actitis hypoleucos	1	0	1.00	1.00	27.0	0	0	17.00	47.75	−	−	−
Alauda arvensis	0	25	0.90	1.00	19.0	0	0	13.92	36.40	0.00	0.00	0.050
Ardea cinerea	0	1	0.00	0.00	50.0	0	1	47.36	1433.00	−	−	1.663
Buteo buteo	0	7	0.29	0.40	52.5	1	0	51.07	806.50	0.05	0.00	0.663
Carduelis cannabina	6	5	0.50	0.00	13.5	1	0	10.87	18.95	0.00	0.01	0.045
C. chloris	4	15	0.70	0.00	14.4	2	0	6.82	27.65	0.00	0.07	0.024
Columba livia	3	0	1.00	0.00	36.0	0	1	3.50	261.00	0.00	0.00	0.197
C. palumbus	7	1	0.38	0.60	33.5	2	0	12.14	494.50	0.13	0.14	0.049
Corvus corone corone	1	12	0.84	0.14	32.2	2	0	74.00	544.50	0.33	0.01	0.656
C. c. cornix	2	0	0.84	0.14	32.2	2	0	27.19	544.50	0.33	0.01	0.656
C. frugilegus	2	3	0.48	0.05	33.0	2	1	34.17	453.50	0.00	0.00	0.764
Cuculus canorus	0	1	0.00	0.67	19.0	1	0	25.57	120.50	0.00	0.00	0.068
Delichon urbica	1	5	0.00	0.60	27.0	0	1	6.34	19.55	0.00	0.00	−
Dendrocopos major	0	1	0.00	0.00	22.0	2	0	11.64	89.65	0.00	0.00	0.072
Emberiza citrinella	8	12	0.83	0.33	12.0	1	0	12.51	26.75	0.05	0.03	0.053
Erithacus rubecula	4	2	1.00	1.00	13.4	2	0	4.99	16.35	0.04	0.01	0.027
Fringilla coelebs	14	23	0.84	0.88	13.9	2	0	8.30	24.20	0.14	0.00	0.036
Hippolais icterina	2	6	0.00	0.00	13.5	2	0	8.05	13.30	0.00	0.07	0.018
Hirundo rustica	8	39	0.03	0.50	19.5	0	1	10.19	19.10	0.01	0.00	0.032
Lanius collurio	1	0	0.00	0.00	14.5	1	0	6.10	30.70	0.02	0.03	0.045
Larus argentatus	0	1	0.00	1.00	37.5	0	1	−	895.00	−	−	0.862
Larus canus	1	7	0.00	1.00	35.0	0	1	−	386.50	−	−	−
L. fuscus	0	1	0.00	1.00	35.0	0	1	25.00	817.50	−	−	−
L. ridibundus	0	4	0.00	1.00	35.0	0	1	−	280.50	−	−	0.514
Luscinia luscinia	1	0	0.00	1.00	9.6	1	0	15.89	25.00	−	−	−
Motacilla alba	2	4	0.76	0.74	13.7	0	0	11.65	20.75	0.39	0.00	0.054
Parus caeruleus	4	0	0.00	0.80	19.0	2	0	5.59	11.75	0.16	0.01	0.027
P. major	4	22	0.07	0.57	18.9	2	0	5.32	18.50	0.03	0.04	0.030
P. palustris	2	4	0.00	0.70	18.5	2	0	6.88	11.90	0.00	0.00	0.027
Passer domesticus	199	261	0.83	0.85	14.1	0	1	3.39	30.35	0.00	0.07	0.043
P. montanus	49	65	0.80	0.90	17.5	1	1	4.91	21.70	0.00	0.13	0.028
Phasianus colchicus	3	5	0.67	1.00	75.0	1	0	62.20	1389.10	0.15	0.50	0.157
Phoenicurus ochruros	1	0	0.00	1.00	15.5	0	0	6.78	16.00	0.00	0.00	0.006
Phylloscopus collybita	4	11	0.00	0.80	15.0	2	0	6.71	7.70	0.04	0.00	0.011
P. trochilus	0	2	0.00	0.20	13.2	2	0	8.06	9.35	0.04	0.01	0.009
Pica pica	1	0	0.67	1.00	27.0	2	0	14.16	228.00	0.45	0.00	0.470
Prunella modularis	3	0	0.00	0.80	11.5	2	0	5.09	18.95	0.06	0.00	0.045
Pyrrhula pyrrhula	0	1	0.09	0.00	15.0	2	0	5.90	31.05	0.05	0.00	0.019
Streptopelia decaocto	1	1	0.83	1.00	17.0	2	0	5.36	201.50	0.00	0.00	0.045
Strix aluco	1	0	0.00	0.00	34.5	2	0	−	491.00	1.00	0.00	0.442
Sturnus vulgaris	1	24	0.12	0.10	21.0	2	1	10.77	80.50	0.01	0.00	0.118
Sylvia atricapilla	3	0	0.00	0.50	11.0	2	0	5.73	18.85	0.01	0.00	0.044
S. borin	2	1	0.00	0.50	11.2	2	0	6.18	19.05	0.04	0.01	0.023
Sylvia communis	5	11	0.00	0.80	11.0	1	0	7.95	14.50	0.01	0.00	0.016
S. curruca	7	4	0.20	0.80	11.0	1	0	4.70	12.40	0.00	0.03	0.029
Troglodytes troglodytes	4	0	0.10	1.00	17.3	2	0	5.51	8.90	0.01	0.00	0.048
Turdus merula	95	35	0.36	0.83	13.6	2	0	7.43	95.85	0.11	0.13	0.237
T. philomelos	2	3	0.40	0.80	13.2	2	0	8.96	70.50	0.30	0.02	0.153
T. torquatus	1	0	0.20	0.80	15.0	2	0	−	117.00	0.44	0.00	0.132

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BACK

Proximate and ultimate factors that promote aggregated breeding in the Western Sandpiper

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Abstract: We report that Western Sandpipers (*Calidris mauri*) on Alaska's Yukon-Kuskokwim River Delta exhibited aggregated breeding behavior at a relatively small spatial scale. Prior to clutch initiation, males performing song flight displays on a 36 ha plot were aggregated as were subsequent initial nesting attempts on the plot. We tested three hypotheses commonly invoked to explain aggregated breeding in territorial species (social mate choice, predation, and material resources hypotheses), and found support for the material resources hypothesis, as dispersed individuals were more often associated with tundra habitat patches, and aggregated individuals nested more often in undulating-tundra habitat patches compared to patch availability. The pattern of habitat occupancy conformed to an ideal despotic distribution with aggregated nesting birds in undulating-tundra patches experiencing lower reproductive success. On our study plot, older, more aggressive males solicited females more often, and defended larger, more dispersed sites in tundra habitat patches, compared to younger, less aggressive males that were aggregated in undulating-tundra habitat patches. Breeding aggregations are often concentrated on or near a critical resource. In contrast, Western Sandpiper breeding aggregations occur when dominant and/or older individuals exclude younger, subordinate individuals from preferred habitat. Although many taxa of non-colonial birds have been reported to aggregate breeding territories, this is the first quantitative report of aggregated breeding behavior in a non-colonial monogamous shorebird species prior to hatch.

Key words: *Calidris mauri;* Space use; Reproduction; Despotic distribution; Material resources hypothesis

导致西滨鹬集群繁殖的直接因子和最终因子

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摘要：该文报道了西滨鹬 (*Calidris mauri*) 在美国阿拉斯加州育空-卡斯科奎姆河三角洲相对较小的空间尺度上所表现的集群繁殖行为。在开始产卵之前, 西滨鹬雄鸟聚集在一处 36 hm^2 的区域鸣唱飞行, 进行求偶炫耀。随后在该区域营巢时, 西滨鹬也保持着集群状态。检验了三个常用于解释具领域行为的物种的集群繁殖的假说：社会成员选择假说、捕食假说和物质资源限制假说。结果表明, 与斑块可利用性相比, 分散的个体常栖息于地势平坦的苔原栖息地斑块, 而集群个体常筑巢于地势起伏的苔原栖息地斑块, 因此, 该研究支持物质资源限制假说。在地势起伏的苔原栖息地斑块集群营巢的西滨鹬繁殖成功率较低, 这表明西滨鹬的这种栖息地占有模式符合理想的等级分布。在研究样地中, 年长且更具攻击性的雄鸟向雌鸟求偶的次数更多, 并且保卫位于地势平坦的苔原栖息地斑块上更大的领域; 相比之下, 年幼且攻击性较弱的雄鸟则聚集在地势起伏的苔原栖息地斑块。通常情况下, 繁殖期的集群多集中于某种关键资源的分布区内或分布区附近, 但西滨鹬繁殖集群的出现是由于年长和处于优势地位的个体将年幼和处于从属地位的个体排斥出高质量的栖息地。虽然, 繁殖领域的集群现象在很多非群居的鸟类中都曾有报道, 但该文是首次对非群居的单配制鸻鹬类物种在孵卵之前的集群繁殖行为进行了定量研究。

关键词：西滨鹬; 空间利用; 繁殖; 等级分布; 物质资源限制假说
中图分类号：Q958.155; Q959.722 **文献标志码：**A **文章编号：**0254-5853-(2011)02-0128-13

Breeding aggregations have been observed in numerous aquatic and terrestrial animals including fish (Itzkowitz, 1978), insects (Muller, 1998; Sumpter & Broomhead, 2000), reptiles (Stamps, 1988), primates

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(Treves, 2000), and birds (Stamps, 1988; Muller et al, 1997). Presumably, animals aggregate when the benefits of doing so exceed the costs of social interaction. The benefits of joining a breeding aggregation may be either resource-based, where (in birds) individuals select habitats that offer foraging opportunities or safe nesting sites (natural selection), or driven by sexual interactions and mate choice (sexual selection hypotheses, Tarof & Ratcliffe, 2004; Tarof et al, 2005). Mechanistic and evolutionary processes that result in avian breeding aggregations have most often been studied among colonial nesting species where nesting and is the primary activity within the aggregation, and among lekking species where only mate choice and reproduction occur (reviewed by Bradbury & Gibson, 1983, Brown & Brown, 2001). Among colonial nesting species, potential costs of nesting in close proximity to conspecifics (increased levels of: resource competition, intraspecific brood parasitism, nest predation, and parasite transmission) appears to be offset by direct benefits including increased food finding efficiency (material resources hypothesis, Kiester & Slatkin, 1974; information center hypothesis, Wittenburger & Hunt, 1985), reduced predation due to group defense or the dilution effect (predation hypothesis, Hamilton, 1971), or increased opportunities for extra-pair copulations (hidden lek hypothesis, Wagner, 1997). Among lekking species, theory on the evolution and maintenance of aggregative behavior suggests individuals aggregate in response to: the patchy distribution of ecological factors (e.g. display sites or predators, material resources and predation hypotheses), the patchy distribution of conspecifics (males cluster in areas where females tend to be found, low-quality males cluster around high-quality males), or because females prefer aggregations of males (social mate choice hypothesis; Allee, 1951; Darling, 1952).

Aggregation of multi-purpose breeding territories is another common form of spatial structure in animals, and occurs when individuals establish territories in close proximity to conspecifics which results in clusters of territories in apparently homogeneous breeding habitat (Tarof & Ratcliffe, 2004). Study of breeding aggregations among socially monogamous avian species (>90% worlds' species; Lack, 1968) has revealed that the spatial distribution of breeding activities is most often correlated with optimal displaying/nesting habitat, areas with high food availability, low predation risk, and species specific foraging and reproductive strategies (material resources, predation, and hidden lek hypotheses; reviewed by Hildén(1965), Cody (1985) and Morse (1989); but see Tarof & Ratcliffe (2004)). Monogamous avian breeding aggregations offer a manageable natural system for testing alternative hypotheses explaining the relative influence of social and environmental factors on the spatial distribution and behavior of individuals. Avian breeding behavior is typically observable, aggregations can be measured accurately and habitat characteristics can be quantified with reasonable effort. Shorebirds (Charadriiformes) exhibit some of the most elaborate and overt breeding displays of any avian group (Miller, 1985). The 24 species of sandpiper in the subfamily Calidridinae (Charadriiformes, Scolopacidae) exhibit every described mating system, with territoriality and mating strategy sometimes varying within a species (Oring, 1982). Studies of intra- and inter-specific variation in calidridine sandpiper social systems have contributed greatly to understanding the evolution of social behavior (Pitelka et al, 1974; Miller, 1979; Oring, 1982; Oring & Lank, 1985). The study of calidridine sandpiper spatial structure offers an opportunity to extend our understanding of how ecological and social factors affect the distribution of breeding animals.

During six years of study in Western Alaska (1999−2001, 2003−2005), we observed apparent aggregation of initial nesting attempts by a territorial calidridine sandpiper, the Western Sandpiper (*Calidris mauri*, Fig. 1). Western Sandpipers are socially and genetically monogamous (i.e., extra-pair paternity is rare) and exhibit biparental care of eggs and young (Holmes, 1971, 1973; Blomqvist et al, 2002). After arriving on the breeding grounds, males establish territories on upland tundra habitat that are defended against conspecifics, from which territorial males advertise for mates using species-specific displays (Brown, 1962; Holmes, 1971). Territories range from 0.2−0.3 ha, and males often defend display territories in close proximity to one another. Territorial males regularly engage in chases and intense fighting; however, after some clutches are completed, it is not uncommon for unpaired males to display over nesting habitat in which females have previously initiated nests (Holmes, 1971; Lanctot et al, 2000). Breeding displays are often performed with one or more other males simultaneously, but not in a duetting fashion (Lanctot et al, 2000). Adult Western Sandpipers obtain some food in the vicinity of their nests but more commonly forage in separate feeding areas along the

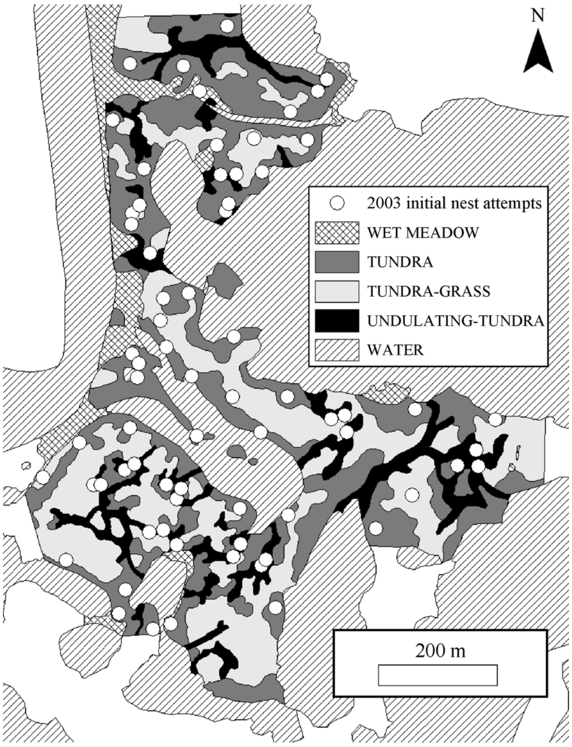

Fig. 1 Habitat map and initial nesting attempts of Western Sandpipers (2003) at the Yukon Delta National Wildlife Refuge's Kanaryarmiut Field Station, Yukon-Kuskokwim River Delta, Alaska (2003). Habitat in white areas was not quantified.

shores of lakes, rivers, and sloughs, and in low-lying marshes (Holmes, 1971; Lanctot et al, 2000).

In our study, we provide statistical support that Western Sandpipers exhibit aggregated breeding behavior. We then evaluate three hypotheses commonly invoked to explain aggregated breeding in territorial animals: (1) The social mate choice hypothesis, which predicts that aggregated males have improved success at attracting social partners compared to solitary individuals; (2) The predation hypothesis, which predicts that aggregated breeding reduces predation via antipredator strategies; and (3) The material resources hypothesis, which predicts that individuals aggregate in response to patchily distributed resources (vegetation and/or food). We tested the social mate choice hypothesis by comparing clutch initiation dates and female age between aggregated and dispersed nesting birds, the predation hypothesis by comparing nest success between aggregated and dispersed nesting birds, and the material resources hypothesis by comparing vegetation associated with aggregated and dispersed nesting birds.

1 Materials and Methods

1.1 Study site

We studied Western Sandpiper breeding behavior at the Yukon Delta National Wildlife Refuge's Kanaryarmiut Field Station, Yukon-Kuskokwim River Delta, Alaska (61°22′N, 165°07′W). Vegetation surrounding Kanaryarmiut Field Station is a complex of lakes, sloughs, wetlands, and upland tundra corresponding to the "lowland moist low scrub" community described by Jorgenson & Ely (2001). Upland tundra vegetation is dominated by lichens, *Sphagnum* spp., *Betula nana*, *Salix fuscescens*, *Ledum decumbens, Empetrum nigrum*, *Rubus chamaemorus*, *Eriophorum* spp., and *Poa eminens*, and wetland and lakeshore margin vegetation is predominately characterized by sedges (*Carex mackenziei*, *C. rariflora*), and grasses (*Poa eminens*, *Calamagrostis* spp., *Eriophorum* spp.; Ely & Raveling, 1984). The upland tundra vegetation community is a mosaic of patches that can be classified into three basic types (Johnson & McCaffery, 2004, Johnson et al, 2009). First is upland tundra that contains graminoid species (hereafter tundra-grass). The second type is upland tundra that lacks a graminoid component (hereafter tundra). The third is undulating-tundra, characterized by greater vertical relief that results in retention of water for longer periods after spring thaw and a sedge and grass component.

1.2 Field surveys

The breeding population of Western Sandpipers at Kanaryarmiut Field Station was continuously monitored for eight years (1998−2005) as part of a long-term demographic study; however, effort varied across years. In 1998 and 2002, demographic data were primarily gathered on a 16 ha plot (1998: 43 nests monitored, 53 adults banded; 2002: 58 nests monitored, 28 adults banded). During the other six years of study at this site (1999−2001 and 2003−2005), data were collected on an additional 20 ha surrounding the original plot "36 ha total; mean ± *SD* number of nests monitored per yr = (113 ± 25), mean ± *SD* number of adults banded per yr = (89 ± 16)". Further, individual behavioral data were recorded on the 36 ha plot during the last three years of study (2003−2005). We only used data gathered during those years when the larger study plot was surveyed because of temporal variation in effort and to maintain consistency in analyses across years. Two to four observers surveyed the 36 ha study plot daily from early May through late July for banded birds, nests, and broods. Adults and chicks were marked with a U.S. Geological

Survey identification band as well as with unique UV-stable color band combinations at the nest. The location and behavior of banded birds was recorded daily (2003−2005). The locations of nests and banded individuals were mapped using ArcMAP (ESRI GIS and mapping software) and nests were monitored through hatch, predation, or abandonment. We produced vegetation maps in the field by manually delineating vegetation patches (tundra, tundra-grass, undulating-tundra) on aerial photographs. Polygons were then digitized and georeferenced using ArcMAP.

1.3 Measures of aggregation

Any classification of random, aggregated, and even distributions in nature comprises arbitrary distinction made along a continuum of three spatial patterns. However, the homogeneous Poisson process is the only point process that is the equivalent of complete spatial randomness (Poole, 1974, Pielou, 1977). Testing for complete spatial randomness relies on comparing an observed spatial pattern with patterns expected for a homogeneous Poisson process. Measures of dispersion may be calculated from the distribution of individuals among sample plots or distances between individuals within a population (nearest neighbor distances; Diggle, 1983). For example, we may calculate nearest neighbor distances for initial nesting attempts on a study plot, then simulate a random distribution with the same number of points within that area, and compare the observed nearest neighbor distances with those expected from a completely random process (i.e., homogeneous Poisson). We plot observed nearest neighbor distances (empirical distribution function, solid line) against hypothetical nearest neighbor distances under complete spatial randomness (cumulative distribution function, straight dashed line) to evaluate whether an observed spatial pattern may have been generated by a completely random process (Fig 2; Dingle, 1983). If a spatial distribution is random there is a straight-line relationship between observed nearest neighbor distances and a completely random distribution (Fig. 2). This straight-line relationship is the probability that empirical nearest neighbor distances take on a value equal to or less than the nearest neighbor distances expected under complete spatial randomness. If our plot of observed nearest neighbor distances falls to the left of the straight line, this indicates there is a greater probability of having nearest neighbor distances less than that under complete spatial randomness, a spatially aggregated distribution (Fig. 2). In contrast, if our plot of empirical data falls to the right of the straight line, this indicates fewer short distances than expected under complete spatial randomness, a spatially even distribution (Fig. 2).

We used the SAS macro collection for nearest neighbor analysis of a spatial point pattern (NNASPP, Schabenberger & Pierce. 2002) to determine whether Western Sandpiper initial nesting attempts were spatially

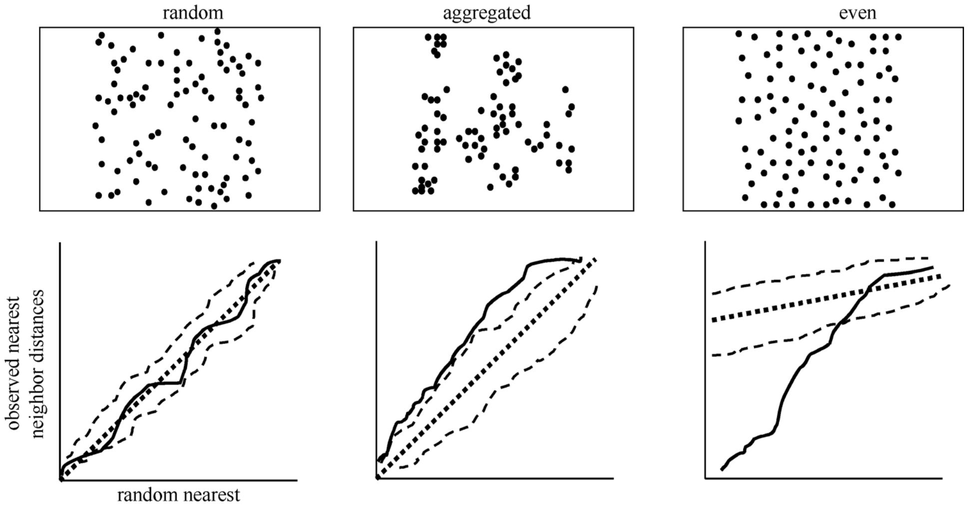

Fig. 2 Three hypothetical spatial distributions (random, aggregated, and even) with corresponding plots of observed nearest neighbor distances along the y-axes (empirical distribution functions, solid line) and nearest neighbor distances expected under complete spatial randomness along the x-axes (cumulative distribution function, straight dashed line). Irregular dashed lines in each plot provide upper and lower simulation envelopes for nearest neighbor distances under complete spatial randomness and represent sample averages.

aggregated on our study plot annually. We modified two macros within this collection to account for the shape of our study plot. We altered the %unitco macro so that it did not scale nest coordinate data to a unit square; instead, this macro plotted nest locations within the specified domain of our 36 ha study plot. We also updated the %hpp macro to simulate a homogenous Poisson processes within the domain of our 36 ha study plot. This macro collection computed nearest neighbor distances for initial nesting attempts on the 36 ha plot each year, simulated 1000 datasets for each year with the same number of nests randomly distributed across the plot to provide an estimate of complete spatial randomness, calculated sample averages for estimates of complete spatial randomness (upper and lower simulation envelopes), and compared observed nearest neighbor distances with estimates of complete spatial randomness using Monte-Carlo significance tests. We also used the SAS macro collection NNASPP to determine if displaying males were spatially aggregated on our study plot on a daily basis during 2003−2005. These data were gathered by two observers simultaneously surveying from the middle of the plot towards its periphery. Care was given to avoid double counting of individuals while surveying the plot. We only recorded the initial location where displaying males were observed. For spatial analysis of displaying males, we selected all days between 10 May and 10 June for which we observed at least 20 displaying males on the plot "average number of days per year ± *SD* = (17 ± 2), mean number of displaying males per day ± *SD* = (27 ± 3)". We did not observe ⩾20 males displaying on the plot in a single day outside of this period.

1.4 Nearest neighbor distance and individual male behavior

We examined individual male behavior and their spatial distribution prior to being paired with a fertile female during 2003−2005. We identified males that were not yet paired with fertile females using nest initiation data (Lanctot et al, 2000). From those, we selected males with a minimum of 10 display flight observations for analyses (minimum of four hours between consecutive observations). This process resulted in the selection of 32 males over a three-year period with a mean of 18 observations/individual. Using these data, we estimated relative display area size for each male by drawing minimum convex polygons around the location of display flights. We also computed the proportion of observations in which males exhibited behavior in five behavioral classes (display flight, chase, fight, solicit, and self-maintenance). We considered a male to have performed a display flight if he vocalized at a height of at least 5 m for a minimum of 10 s, chasing behavior entailed a male flying after one or more conspecifics, physical contact with a conspecific denoted fighting behavior, the tail-up courtship stance described by Holmes (1973) was used to quantify solicitation, and self-maintenance behaviors included loafing, sleeping, and preening. As a measure of spatial dispersion, we calculated the distance from each initial nesting attempt on the plot to its two nearest neighbors using ArcMAP. We then examined the relationship between male behaviors prior to being paired with a fertile female and the sum of the distances from each male's initial nesting attempt to the two nearest neighboring nests using Spearman rank correlation (Zar, 1999).

1.5 Testing the Material Resources hypothesis

1.5.1 Habitat use in relation to availability

To examine the relationship between spatial dispersion and habitat patches (tundra, tundra-grass, undulating-tundra), we delineated aggregated and dispersed nesting birds by separating nearest neighbor distances (sum of the distance from each nest to its first two nearest neighbors) into quartiles annually. This resulted in nearly a three-fold difference in nearest neighbor distances between the first and fourth quartiles or aggregated and dispersed nesting birds (Tab. 1). We then overlaid initial nesting attempts on our vegetation map (Fig. 1), and calculated the number of nests within each habitat class to determine whether aggregated (1st nearest neighbor distance quartile) and dispersed (4th nearest neighbor distance quartile) nesting birds differentially nested in specific habitat patches. We compared the number of aggregated and dispersed nesting birds in each habitat type annually to the number of nests expected in each habitat type if birds utilized habitat in relation to availability using chi-square goodness of fit tests (Zar, 1999). Similarly, we evaluated the locations where the earliest arriving males (first five days males were observed displaying each year) were observed performing display flights. We compared the number of displaying males in each habitat patch type to the number of males expected in each habitat type if birds utilized habitat in relation to availability using chi-square goodness of fit tests. We also examined male and female age in relation to initial nest placement among the

Tab. 1 Sum of distances between initial Western Sandpiper nesting attempts and two nearest neighbor nests on a 36ha plot at Kanaryarmiut Field Station, Yukon-Kuskokwim Delta, Alaska (1999−2001, 2003−2005).

Quartile (*N*)	Median (m)	Mean (m) ± *SD*	Range (m)
1 (120)	52	50 ± 15	13−74
2 (120)	75	75 ± 9	53−97
3 (117)	99	98 ± 12	75−124
4 (121)	137	147 ± 36	102−278

three habitat patch types (tundra, tundra-grass, undulating-tundra). We grouped birds into three age classes for this analysis (minimum age, number of years observed breeding at the site = 1, 2, ⩾3). We randomly selected a single nesting observation for birds observed in multiple years for this analysis to avoid pseudoreplication, and used chi-square goodness of fit tests to determine if habitat patch use among age classes varied from that expected based on availability.

1.5.2 Microhabitat associated with nests

During 2004, we examined microhabitat associated with Western Sandpiper nests (N = 128) by comparing the proportion of five vegetation types (birch, grass, herb, moss, lichen) and the amount of vertical relief within a 1 m^2 frame centered on each nest and a random point within 40 m of each nest. We used matched-pairs logistic regression to examine microhabitat variation between nest sites and associated random points (Johnson & Oring, 2002). We compared potential models beginning with a model containing all six predictor variables and compared this model's fit with simpler models to achieve the most parsimonious regression model that accurately represented the data. Akaike information criteria (AIC) were computed for each model to compare model ranks and weights in determining the likelihood of each model given the data (Burnham & Anderson, 1998; Anderson et al, 2000).

1.6 Testing the social mate choice hypothesis

1.6.1 Minimum age in relation to nest dispersion

We used contingency tables to examine the relationship between Western Sandpiper minimum age and nest dispersion (Zar, 1999). We constructed a 2 x 3 contingency table for each sex with aggregated (1st nearest neighbor distance quartile) and dispersed (4th nearest neighbor distance quartile) nesting birds as rows and minimum age (number of years observed breeding at the site = 1, 2, ⩾3) as columns to test whether Western Sandpiper age was independent of nest dispersion.

1.6.2 Clutch initiation date in relation to nest dispersion and habitat

We used SAS PROC MIXED to compare mean clutch initiation date, for initial nesting attempts between aggregated and dispersed nesting birds using analysis of variance (ANOVA, Littell et al, 2002). Initiation date was the dependent variable in the model, and nest dispersion was a two-level fixed factor independent variable (aggregated = 1st nearest neighbor distance quartile, dispersed = 4th nearest neighbor distance quartile). We also included year as a random factor in the model to control for annual variation. Residuals were normally distributed (Shapiro-Wilk tests $P > 0.10$) and had homogeneous variance after a square root transformation. We compared mean initiation date using Least Square Means ($\alpha = 0.05$). Based on habitat analyses, we also performed an a posteriori analysis comparing mean clutch initiation date between birds that nested in or out of undulating-tundra habitat while controlling for year effects. This analysis was similar to that described above except the independent variable was a two-level fixed factor (nests in undulating-tundra habitat, nests *not* in undulating-tundra habitat).

1.7 Testing the predation hypothesis

We compared nest success between aggregated and dispersed nesting birds using logistic regression. For this model, the dependent variable, nest success (at least one egg hatched in a clutch), was a binomial response (1 = successful, 0 = unsuccessful). Nest dispersion was a categorical variable with two levels (aggregated = 1st nearest neighbor distance quartile, dispersed = 4th nearest neighbor distance quartile), and we included year (categorical) and initiation date (continuous) as covariates in the model as these factors are known to influence nest success in many avian species (Lack, 1954; Martin, 1987). Based on habitat analyses, we also performed an a posteriori analysis examining nest success between habitat types. As described above, we used logistic regression to model the probability of nest success based on whether birds nested in or out of undulating-tundra habitat while controlling for initiation date and year effects. In this model, habitat type was a categorical variable with two levels (undulating-tundra, not undulating-tundra).

2 Results

During six years of study (1999−2001 and 2003−2005), we individually color banded 453 adult

Western Sandpipers and located and monitored 680 nests. Four hundred and thirty-three of these nests were initial nesting attempts on the 36 ha plot (mean number of initial nesting attempts per year ± *SD* = (72 ± 10).

2.1 Aggregation patterns

Displaying males exhibited an aggregated spatial distribution, and subsequent initial nesting attempts attended by those males also were aggregated. Displaying males exhibited an aggregated spatial distribution on the study plot during >80% of observation days when we observed ⩾ 20 displaying males (2003, 83% of observation days, N = 18d, MC significance tests $P < 0.01$ = 10d, $P < 0.05$ = 5d, $P > 0.05$ = 3d, 1000 simulations/d; 2004, 82% of observation days, N = 17d, MC significance tests $P < 0.01$ = 11d, $P < 0.05$ = 4d, $P > 0.05$ = 3d, 1000 simulations/d; 2005, 87% of observation days, N = 15 d, MC significance tests $P < 0.01$ = 10d, $P < 0.05$ = 3d, $P > 0.05$ = 2d, 1000 simulations/d). Western Sandpiper initial nesting attempts were spatially aggregated on the 36ha plot throughout the course of this study (1999, $\chi^2 = 31.0$, $P < 0.001$, $N = 49$; 2000, $\chi^2 = 36.2$, $P < 0.001$, $N = 84$; 2001, $\chi^2 = 35.2$, $P < 0.001$, $N = 85$; 2003, $\chi^2 = 41.8$, $P < 0.001$, $N = 69$; 2004, $\chi^2 = 38.0$, $P < 0.001$, $N = 83$; 2005, $\chi^2 = 39.0$, $P < 0.001$, $N = 63$; 1000 simulations/yr). The observed distribution of nearest neighbor distances for initial nesting attempts in 2003 (Fig. 1) indicated a spatially aggregated distribution (Fig. 3). The plot of observed nearest neighbor distances (solid line, Fig. 3) falls to the left of the straight line relationship expected under complete spatial randomness (straight dashed line, Fig. 3) and is outside the simulation envelope for complete spatial randomness (irregular dashed lines, Fig. 3) indicating significant spatial aggregation. For brevity, we present the map of initial nesting attempts and plot of nearest neighbor distribution against complete spatial randomness for a single year (2003; Fig. 1,3); the comparable results for the remaining five years of study were similar.

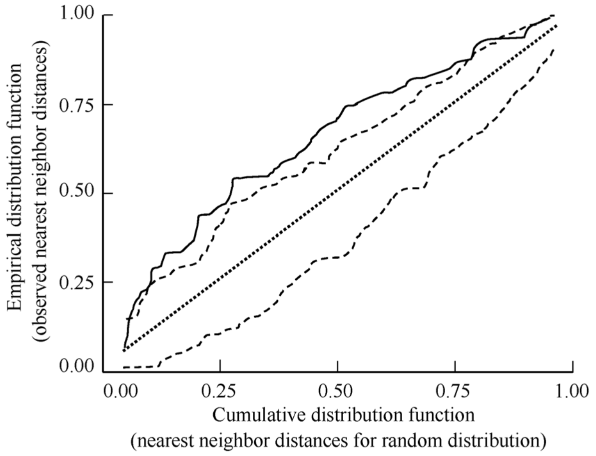

Fig. 3 Plot of the empirical distribution function of observed nearest neighbor distances for Western Sandpiper initial nesting attempts on the study plot in 2003 (solid line) versus the cumulative distribution function of a hypothetical distribution of nearest neighbor distances under complete spatial randomness (straight dashed line). Irregular dashed lines provide upper and lower simulation envelopes for the cumulative distribution function based on 1000 Monte Carlo simulations.

2.2 Nearest neighbor distance and individual male behavior

Dispersed nesting males performed song-flight displays over a relatively larger area compared to aggregated nesting males prior to being paired with a fertile female (Fig. 4). Dispersed nesting males also were observed chasing conspecifics and soliciting females more often compared to aggregated nesting males (Fig. 4). There was no correlation between nearest neighbor

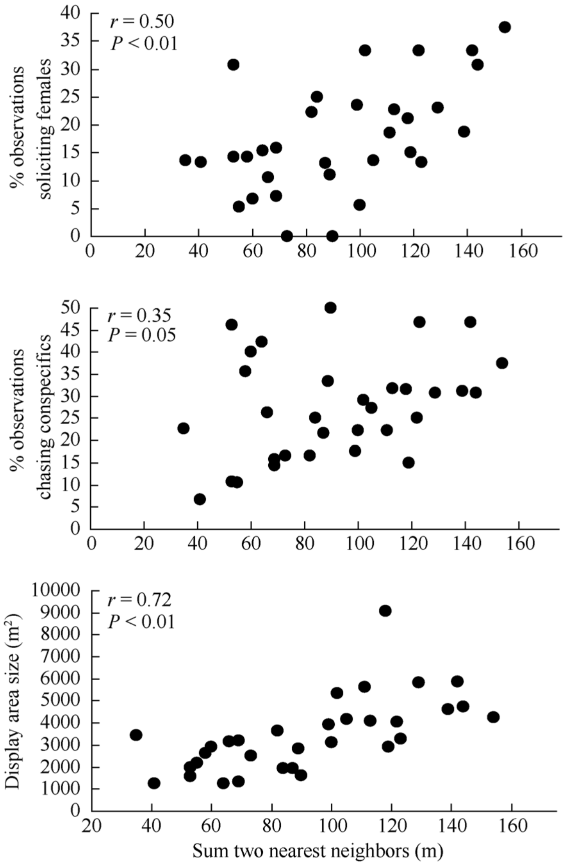

Fig. 4 Spearman rank correlations between individual male (N = 32) behaviors (proportion of observations observed soliciting females and chasing conspecifics, and display area size) prior to being paired with a fertile female and the sum of the distances from subsequent initial nesting attempts to the two nearest neighbor nests (2003−2005).

distances and the number of song-flight displays, amount of fighting, or self-maintenance behavior observed (all $r \leqslant 0.2$, all $P > 0.25$, $N = 32$).

2.3 Material resources hypothesis

2.3.1 Habitat use in relation to availability

During 2003−2005, the earliest arriving males displayed more often over tundra habitat and less often over undulating-tundra habitat than expected if birds utilized habitat patches in relation to availability (Fig. 5). Among initial nesting attempts, dispersed nests were more often in tundra habitat patches, less often in tundra-grass, and occurred in relative proportion to availability of undulating-tundra (Fig. 6). Whereas, aggregated initial nesting attempts were observed more often in undulating-tundra habitat patches, less often in tundra, and in relative proportion to availability in tundra-grass (Fig. 6). Younger males were more often associated with nests in undulating-tundra habitat patches, less often in tundra, and in relative proportion to availability in tundra-grass (Fig. 7). In contrast, older males were more often associated with nests in tundra habitat patches, less often in tundra-grass, and were never observed nesting in undulating-tundra (Fig. 7). Regardless of age, initial nesting attempts in the three habitat patches did not vary from that expected if females utilized habitat patches in relation to availability (1yr $\chi^2_{0.05,2} = 2.1$, $P > 0.25$, $N = 89$, 2yr $\chi^2_{0.05,2} = 1.1$, $P > 0.50$, $N = 27$, ⩾3yrs $\chi^2_{0.05,2} = 0.6$, $P > 0.50$, $N = 13$).

2.3.2 *Microhabitat associated with nests*

Matched-pairs logistic regression revealed the proportion of birch (all models, $\chi^2_1 \geqslant 11.1$, $P < 0.001$) and graminoids (four top-performing models, $\chi^2_1 \geqslant 7.4$, $P < 0.01$) within 1 m^2 (all other predictor variables, $\chi^2_1 \leqslant 1.0$, $P > 0.5$, Tab. 2) were the dominant microhabitat predictors of nest presence. The top-performing model contained only birch and graminoids and this model had > 2 times the support of the next best performing candidate model (Tab. 2). There was a consistent positive association of birch and a negative association

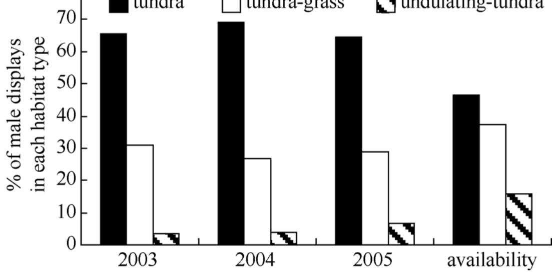

Fig. 5 Proportion of male Western Sandpiper display-flights observed over three habitat patch types during the first five days males were observed displaying on the study plot annually (2003−2005)

Habitat use by displaying males differed significantly from that expected if birds utilized habitat patches in relation to availability (2003 $\chi^2_{0.05,2} = 5.4$, $P < 0.10$, $N = 29$; 2004 $\chi^2_{0.05,2} = 6.0$, $P < 0.05$, $N = 26$; 2005 $\chi^2_{0.05,2} = 6.4$, $P < 0.05$, $N = 45$).

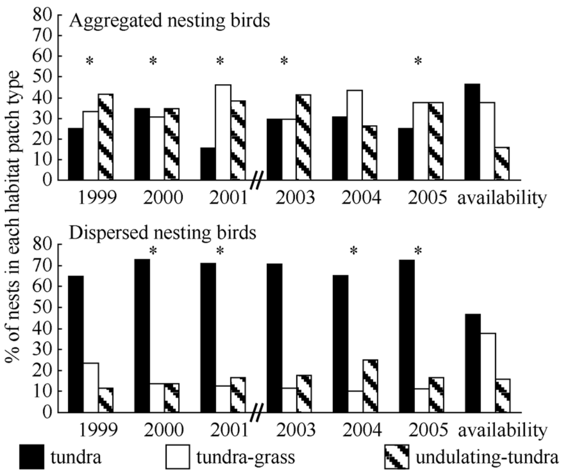

Fig. 6 Proportion of initial nesting attempts by aggregated and dispersed nesting birds in three habitat patch types on a 36 ha plot annually (1999−2001, 2003−2005)

Habitat use for both aggregated and dispersed nesting birds differed significantly from that expected if birds utilized habitat patches in relation to availability (* = $P < 0.05$). Aggregated nesting birds: 1999 $\chi^2_{0.05,2} = 6.3$, $P < 0.05$, $N = 12$, 2000 $\chi^2_{0.05,2} = 6.2$, $P < 0.05$, $N = 23$, 2001 $\chi^2_{0.05,2} = 14.3$, $P < 0.001$, $N = 26$, 2003 $\chi^2_{0.05,2} = 8.2$, $P < 0.025$, $N = 17$, 2004 $\chi^2_{0.05,2} = 3.0$, $P > 0.10$, $N = 23$, 2005 $\chi^2_{0.05,2} = 6.3$, $P < 0.05$, $N = 16$; Dispersed nesting birds: 1999 $\chi^2_{0.05,2} = 2.3$, $P > 0.25$, $N = 17$, 2000 $\chi^2_{0.05,2} = 6.6$, $P < 0.05$, $N = 22$, 2001 $\chi^2_{0.05,2} = 7.0$, $P < 0.05$, $N = 24$, 2003 $\chi^2_{0.05,2} = 5.1$, $P < 0.10$, $N = 17$, 2004 $\chi^2_{0.05,2} = 6.5$, $P < 0.05$, $N = 20$, 2005 $\chi^2_{0.05,2} = 5.9$, $P < 0.05$, $N = 18$.

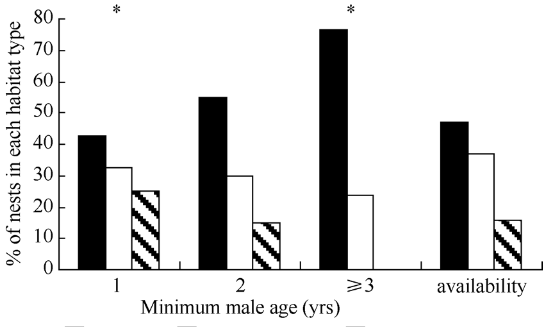

Fig. 7 Proportion of initial nesting attempts in three habitat patch types in relation to minimum male age (# yrs observed breeding at the site)

Habitat use for the youngest and oldest age classes (1^{st} year and ≥ 3 years, respectively) differed significantly from that expected if birds utilized habitat patches in relation to availability (* = $P < 0.05$, 1yr $\chi^2_{0.05,2} = 12.2$, $P < 0.01$, $N = 201$, 2yr $\chi^2_{0.05,2} = 0.6$, $P > 0.95$, $N = 20$, ≥ 3yrs $\chi^2_{0.05,2} = 6.8$, $P < 0.05$, $N = 17$).

Tab. 2 Multi-model inference based on results from matched-pair logistic regression of Western Sandpiper nest sites and matched random points

Model	AIC	Δ_i	w_i	Odds ratio	
				Birch	Graminoids
birch, graminoids	154.62	0.0	0.58	1.08	0.95
birch, graminoids, herbs	156.22	1.6	0.26	1.08	0.95
birch, graminoids, herbs, relief	158.12	3.5	0.10	1.08	0.95
birch, graminoids, herbs, relief, moss, lichen	160.02	5.4	0.04	1.09	0.96
birch	161.79	7.2	0.02	1.08	—

Model parameters denote the proportion of each vegetation type within 1m^2 of nest sites and matched random points. Δ_i is the rank of each model by rescaling AIC values such that the model with the minimum AIC value has a value of zero, and w_i is the likelihood of the model given the data. Odds ratios indicate percentage increase (birch) or decrease (graminoids) in the odds of a nest being present (i.e. 8%−9% increase in the odds of a nest being present when birch was present, 4%−5% decrease in the odds of a nest being present when graminoids were present).

of graminoids with nest sites compared to random points in the four top-performing models (Tab. 2; range of odds ratios, birch = 1.08−1.09, graminoids = 0.95−0.96).

2.4 Social mate choice hypothesis

2.4.1 Minimum age in relation to nest dispersion

Results did not indicate a difference in male or female age between aggregated and dispersed nests (males $\chi^2_{0.05,\,2}$ = 3.10, $P > 0.10$, $N = 238$, females $\chi^2_{0.05,\,2}$ = 1.59, $P > 0.25$, $N = 129$).

2.4.2 *Clutch initiation date in relation to nest dispersion and habitat*

Mean clutch initiation date was June 1st “mean Julian date ± SE all years combined = (152 ± 2)”.

There was no difference in mean clutch initiation dates between aggregated and dispersed nests (t_{213} = −1.50, P = 0.14), or between nests located in or out of undulating-tundra habitat (t_{426} =−0.91, P = 0.36).

2.5 Predation hypothesis

Logistic regression did not indicate that nest success significantly varied between aggregated and dispersed nesting birds (χ^2_1 = 0.02, P = 0.90, N = 220); however, there was significant annual variation in nest success during the course of study (χ^2_5 = 11.76, P = 0.04, N = 220). The annual percentage of aggregated nests that hatched ranged between 1%−36% and the percentage of dispersed nests that hatched annually ranged between 11%−43%. The logistic regression model examining nest success between habitat types indicated that nest success varied between nests located in and out of undulating-tundra habitat (Fig. 8, χ^2_1 = 4.2, P = 0.04, N = 433). Nests that were *not* in undulating-tundra patches were 63% more likely to hatch compared to nests within undulating-tundra patches (odds ratio = 1.63, 95% Wald confidence limits 1.02−2.61).

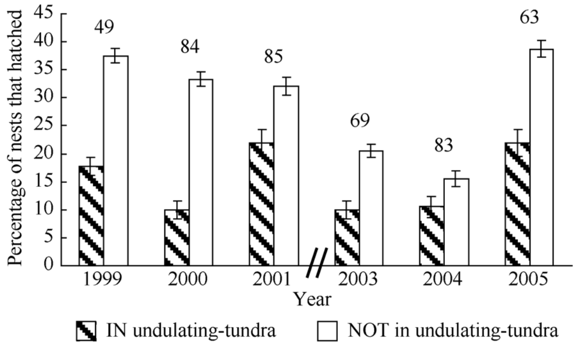

Fig. 8 Percentage of Western Sandpiper initial nesting attempts to hatch (± *SD*) in two habitat categories annually on a 36ha study plot at Kanaryarmiut Field Station, Yukon-Kuskokwim River Delta, Alaska

Numbers above bars indicate sample sizes.

3 Discussion

Western Sandpipers exhibited aggregated breeding behavior at a relatively small spatial scale (36 ha). Prior to clutch initiation, male song flight displays were spatially aggregated and subsequent initial nesting attempts on the plot also were. Although many taxa of non-colonial birds have been reported to aggregate breeding territories (Stamps, 1988; Reed & Dobson, 1993; Cade & Woods, 1997; Danchin & Wagner, 1997; Reed, 1999; Etterson, 2003;Tarof et al, 2004), to our knowledge, this is the first study to quantify aggregated breeding behavior in a non-colonial monogamous shorebird species prior to hatch.

3.1 Social mate choice hypothesis

If sexual selection favors male aggregation because it facilitates social mate choice (Allee, 1951; Darling, 1952), then breeding aggregations of Western Sandpipers may represent an adaptive male strategy. Facilitation of mate choice would be especially important among birds in which female choice is constrained temporally because of a compressed breeding season (Veen et al, 2001) or when male parental care is important (Gowaty, 1996), such as in the Western Sandpiper.

We would expect aggregated males to acquire a mate (and subsequent clutch) earlier than more dispersed individuals if aggregated males are more attractive than solitary males, or if unpaired females more easily detect aggregated males (Real, 1990). We failed to find support for the social mate choice hypothesis in Western Sandpipers as mean clutch initiation date did not vary between aggregated and dispersed nesting birds. Because of the time constraints associated with arctic breeding, it is possible that there is little-to-no opportunity for substantial variation in clutch initiation date for Western Sandpipers (Johnson & Walters, 2008; Johnson et al, 2010). Regardless of potential temporal constraints on clutch initiation date, male aggregations could still facilitate social mate choice if aggregated males were able to attract higher quality females compared to dispersed individuals. However, we found no evidence that more experienced females were associated with aggregated nests compared to dispersed nests.

3.2 Predation hypothesis

We failed to find support for the predation hypothesis as an explanation for aggregated breeding in Western Sandpipers. The predation hypothesis (Hamilton, 1971; Pulliam, 1973) predicts that bird's aggregate because clustering of individuals reduces predation via proximate antipredator mechanisms. However, results from six years of data revealed no consistent variation in nest success between aggregated and dispersed nesting birds.

3.3 Material resources hypothesis

The material resources hypothesis predicts that individuals aggregate in response to patchily distributed resources (vegetation and/or food, Kiester & Slatkin, 1974). We found support for the material resources hypothesis in that aggregated nests were more often associated with undulating-tundra habitat patches and dispersed nests were more often in tundra patches. The disproportionate use of undulating-tundra patches by aggregated birds resulted in a reduction in their use of tundra patches, but they did place nests in tundra-grass patches in relative proportion to habitat availability. In contrast, as a result of their disproportionate use of tundra patches, dispersed nesting birds used tundra-grass habitat patches less than expected, but used undulating-tundra habitat patches in relative proportion to availability.

Previous investigations have suggested that social organization, territorial behavioral, and nest dispersion have coevolved to increase a species' ability to exploit resources (food, habitat, and mates) over both space and time (Holmes, 1966, 1972; Oring & Knudson, 1972; Graul, 1973; Pitelka et al, 1974; Safriel, 1975; Emlen & Oring; 1977). Among monogamous Arctic breeding sandpipers, such as the Western Sandpiper, it has been assumed "…that most if not all species in this group are dispersed relatively evenly over the available habitat each year." (Pitelka et al, 1974). Although territory size, and subsequently breeding density, may vary as a result of whether food is primarily acquired on (Dunlin, *C. alpina*) or off (Western Sandpiper) the nesting territory (MacLean, 1969; Soikkeli, 1967; Holmes, 1970, 1971), large fluctuations in densities within a species at particular sites have not been reported (Pitelka et al, 1974). Holmes (1971) suggested that high densities of Western Sandpipers in some areas of western Alaska are related to the patchy distribution of suitable nesting habitat (upland tundra; dwarf shrub-heath tundra in Holmes (1971)). As a result, Holmes (1971) reported that the overall distribution of Western Sandpiper in western Alaska is clumped, but within suitable nesting habitat birds are regularly dispersed. Our results are contrary to this observation. Although Holmes' study site was merely 30 km northwest of ours, it is possible that upland tundra vegetation was more homogeneous at his site compared to ours, and this could result in the discrepancy in observed breeding distribution between studies. Holmes (1971) did not delineate vegetation patches within upland tundra habitat as we did, thus we are not able to compare upland tundra vegetation community composition between the two sites.

3.4 Ideal free and ideal despotic distributions

Our results can be interpreted in terms of the theory of ideal free and ideal despotic distributions (Fretwell & Lucas, 1970; Fretwell, 1972). In situations conforming to the ideal free distribution, animals move freely among habitats and assort themselves in proportion to resource availability. However, once a critical density is attained in preferred habitats, individual fitness is reduced in preferred habitats and individuals begin to colonize less preferred habitat where competition is less. This results in individual fitness being equal over a range of habitats, resources, or other conditions. Alternately, the ideal despotic distribution model predicts that subordinate individuals are constrained in their choice of habitat by dominant individuals (Messier et al, 1990), resulting in differences in fitness among habitats. Primary assumptions of this model are that different habitats provide varying opportunities for individual fitness, and that competition will ensue where resources are limited (Leibold, 1995). Based on our observations that dispersed individuals more often nested in tundra habitat patches (Fig. 6), displayed over larger areas, chased conspecifics and solicited females more often (Fig. 4), that the earliest arriving males primarily displayed over tundra and tundra-grass habitat patches (Fig. 5), and that older males nested in tundra and tundra-grass but not in undulating-tundra patches (Fig. 7), we conclude that there is competition among males for tundra and tundra-grass habitat patches.

For the breeding distribution of Western Sandpipers to conform to an ideal deposit distribution, fitness must vary among habitat patches. On our study plot, nests in tundra and tundra-grass habitat patches that males appeared to prefer were more likely to hatch compared to nests in undulating-tundra patches (Fig. 8). We can only speculated as to why nest success was lower in undulating-tundra patches, but we did observe mink (*Mustela vison*) regularly using these patches to move across the landscape from one lakeshore to another, and both Arctic (*Alopex lagopus*) and red (*Vulpes vulpes*) fox commonly used vertical structure, such as frost heaves, to apparently surprise prey while foraging near the study site. Greater vertical relief associated with undulating-tundra patches also may provide such concealment for foraging fox on our study plot. Regardless of the mechanism(s) underlying variation in reproduction, we conclude that Western Sandpipers exhibited a despotic breeding distribution on the study-plot, with subordinate males forced to aggregate their nests in undulating-tundra habitat patches where fitness is reduced. We typically think of breeding aggregations as being concentrated on or near a critical resource, Western Sandpiper breeding aggregations appear to result from dominant and/or older individuals excluding younger, subordinate individuals from preferred habitat.

3.5 Microhabitat associated with nests

There is one intriguing inconsistency in our interpretation of our results. Dispersed males nested in tundra habitat patches more often than expected based on availability, less often in tundra-grass than expected, but in relative proportion to availability of undulating-tundra patches. If nesting in undulating-tundra resulted in reduced fitness via lower nest success, why were older, more aggressive, males utilizing undulating-tundra at all? Why were these individuals not utilizing tundra and tundra-grass patches to the exclusion of undulating-tundra? Analysis of nest site microhabitat features revealed that Western Sandpiper nests were more often associated with areas containing a higher percentage of dwarf birch and a lower percentage of graminoid species. It is reasonable to suppose that reduced use of tundra-grass patches by dispersed nesting birds, but continued use of undulating-tundra patches, is the result of birds avoiding graminoid species and preferentially placing nests near dwarf birch. However, such reasoning does not explain nest placement among aggregated nesting birds, as those birds used tundra-grass habitat patches in relative proportion to availability, but reduced their use of tundra patches. Continued use of tundra-grass and reduced use of tundra patches by aggregated individuals may be the result of aggregated individuals making the best of a bad situation. Aggregated males appeared to be subordinate to dispersed individuals, so they may have been excluded from using habitat other than tundra-grass and undulating-tundra patches.

4 Conclusions

Western Sandpipers exhibited a spatially aggregated breeding distribution on a 36 ha plot. Displaying males were aggregated on a daily basis as were initial nesting attempts on an annual basis. We found support for the material resources hypothesis, as dispersed individuals were more often associate with tundra habitat patches, and aggregated individuals nested more often in undulating-tundra patches. There also was support for an ideal despotic distribution with lower reproductive success associated with aggregated nesting birds in undulating-tundra patches. Although we may typically think of breeding aggregations as being concentrated on or near a critical resource, Western Sandpiper breeding aggregations appear to result from dominant and/or older individuals excluding younger, subordinate individuals from preferred habitat.

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斑背大尾莺繁殖期鸣声行为分析

BACK

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摘要：2009 年 5—7 月，在辽宁双台河口保护区录制了 20 只繁殖期斑背大尾莺雄性个体的鸣声。根据行为特征，该鸟鸣声定义为 3 种鸣声类型：求偶炫耀鸣唱、报警声和联络声。利用 Wavesurfer 软件对 20 只斑背大尾莺雄性个体 543 个鸣声的句子持续时间、句子音节个数、音节持续时间、音节间隔时间等 4 个参数进行分析测量，发现求偶炫耀鸣唱由节奏逐渐加快的前部句子和音节组成复杂的主体部两个句子组成；报警声和联络声的句子均由单音节组成。音节类型总数为 38 种，其中包括前部句子的音节类型 6 种。采用单因素方差分析(one–way ANOVA)对求偶炫耀鸣唱的 4 个参数进行差异性检验发现，不同个体的各个参数均呈极显著差异($P<0.01$)。

关键词：鸣声行为；斑背大尾莺；节奏
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Analyzing Japanese marsh warbler (*Megalurus pryeri*) song behavior in the breeding season

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Abstract: The songs of Japanese marsh warblers (*Megalurus pryeri*) were recorded during May to July in 2009 at Shuangtaihekou Nature Reserve, Liaoning, China. Based on song characteristics, songs were divided into three types: courtship songs, alarm calls or contact calls. We analyzed and measured four parameters from 543 verses recorded from 20 males. The parameters were: duration of verse, number of syllables, duration of syllable, and interval of syllable. Verses of courtship song are formed of two verses, the first part's rhythm is more and more quick with time; the main body part is formed with complex syllables. Alarm calls and contact calls are simple, and formed with simple and repeat syllables. All songs contained 38 syllable types (six syllable types of the first part included). Acoustic features of the courtship song were statistically different, as was the calls of each individual.

Key words: Song behavior; Japanese marsh warbler; *Megalurus pryeri*; Rhythm

鸟类的鸣声包括鸣叫和鸣唱(Catchpole & Slater, 2008)，通常被认为是一种积极的信号(McDonald, 1989; Searcy & Beecher, 2009)，可以促进占据领域的个体成功地获得和享用资源(Eriksson & Wallin, 1986)、吸引配偶(Mountjoy & Lemon, 1991)、保卫领域等(Catchpole & Slater, 2008)。繁殖期鸟类的鸣声复杂多样，同时与各种行为活动相关(Lei et al, 2003; Catchpole & Slater, 2008)，求偶炫耀和领域保护的鸣声是鸟类鸣声中最常见的类型(Kunc et al, 2005)。通过鸟类鸣声和相应行为的研究，可以了解鸟类不同鸣声的生物学意义，以及鸣声与行为的相互关系(Guo et al, 2007)。鸣声研究还可应用到分类学等领域，为鸟类分类地位的确定提供佐证(Lei & Wang, 2002; Zhang et al, 2006)。

斑背大尾莺(*Megalurus pryeri*)是东亚特有鸟类，有两个亚种——亚种 *pryeri* 和 *sinensi*，它们分别繁殖于日本本州岛北部和中国东北。2009 年，IUCN 世界濒危物种红皮书将斑背大尾莺列为近危物种(NT)。迄今对斑背大尾莺的研究主要有数量、分布、栖息地调查(Nagata, 1997; Lu & Li, 1997; Gan et al,

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2006)、繁殖生态学研究(Li & Wang, 2006)、分类地位和遗传多样性研究(Drovetski et al, 2004; Zhang, 2007; Zhang et al, 2010); 而关于其鸣声方面仅见简单的描述(Chang et al, 1995; Mackinnon et al, 2000)。本文对斑背大尾莺鸣声进行了研究, 初步分析了其鸣声特点和相应的行为特征, 为基于鸣声方面更加深入地研究提供启示和线索。

1 研究地区概况

双台河口保护区位于辽宁省盘锦市境内, 地处辽东湾顶端, 双台子河入海处, 地理坐标介于东经121°30′~122°00′, 北纬 40°45′~41°10′, 总面积 8 万 hm^2, 其中芦苇有 2.7 万 hm^2, 是世界上面积较大的芦苇沼泽湿地。地势北高南低, 最高海拔仅 5.7 m。处于北温带半湿润季风区, 四季分明。年均气温 8.4℃, 年均降水量为 623.2 mm, 植物区系特征属华北植物区, 区内木本植物较少, 植物种类比较单一。主要的植被类型为: 滨海碱蓬盐生草地、獐矛盐生草甸、沼泽植被和水生植被。其中, 植被组成分布最广的是沼泽植被。主要有 3 种形式, 第一种为生长有茂密的芦苇, 杂有少量的水烛(*Typha angustifolia*)、萤蔺(*Scirpus juncoides*)等; 第二种以芦苇为主, 明显分布有香蒲(*Typha latifolia*)、水烛等; 第三种植被稀疏但物种繁多, 主要植物有香蒲、泽泻(*Alisma orientale*)、灯心草(*Juncus effusus*)和菖蒲(*Acorus calamus*)(Qiu, 1998; Yang et al, 1998)。

2 方 法

2.1 鸣声采集

2009 年 5—7 月, 利用 lotoo L-200 录音机(北京世纪乐图数字技术有限责任公司, 北京; 录音范围为 20~2 万 Hz; 16 bit/48 kHz), SGM 1X 强定向话筒(AZDEN, 阿兹丹; 日本; 响应频率范围为 80~1.8 万 Hz), 在双台河口保护区录制繁殖期斑背大尾莺 20 只雄性个体的鸣声, 并用 Sony HDR-SR11E (日本)数码摄录机录制行为。选择晴天无风日子, 上午 4：30 到 11：00, 下午 14：00 到 17：00 进行鸣声录制。录音时, 录音者手持定向话筒, 隐蔽好后, 每只个体鸣声录制的时间至少为 1 min。

2.2 个体领域标记

斑背大尾莺进入繁殖期后, 领域非常固定, 几乎整个繁殖期都停在固定的一根非常显著的枯芦苇枝或小树枝上。两只个体常停留的枯芦苇枝或小树枝之间直线距离最短约为 20 m。根据这个特点, 在其停留的枯芦苇枝或小树枝附近突出的芦苇或草上打结作标记。另外, 在打结处的芦苇或草上系塑料绳。塑料绳颜色为红色, 便于与周围环境区分。绳宽约 1 cm, 标记时绳长自定。绳上用黑色记号笔标有标记日期, 个体编号与 GPS 坐标。标记方法已进行预实验, 证明这种标记法对斑背大尾莺的活动没有影响。在两个月的研究时间内, 绳上的标记没有褪色。

2.3 鸣声术语定义

鸣叫(call)：鸟类发出的短的、简单的鸣声, 雌雄个体全年都会鸣叫, 包括飞行叫声、报警声、乞食声和集群声等(Baker, 2001)。鸣唱(song)：雄性个体在繁殖期发出的长时间的、复杂的鸣声(Catchpole & Slater, 2008)。音素(note/element)：声谱图上一段连续的曲线痕迹, 是鸣声的最基本结构(Päckert et al, 2004)。音节(syllable/element-group)：一个或多个独立的音素固定组合在一起构成音节, 通常在句子中重复多次(Tracy & Baker, 1999; Päckert et al, 2004)。音节型(syllable type)：音节的形态特征, 主要包括音素的组成和排列顺序(Xiao et al, 2008)。句子(verse/phrase/motif)：一个或多个音节的重复集合构成句子(Leonardo & Konishi, 1999)。句式(synax)：音素或音节在句子中的排列顺序(Päckert et al, 2004)。节奏(rhythm)：音节的持续时间和间隔时间, 代表了句子的节奏特征(Thorpe & Hinde, 1969)。

2.4 鸣声参数测量和统计

录制“*.wav”(16 bit/48 kHz)格式的各种鸣声导入笔记本电脑, 选择清晰的 543 个鸣声, 利用 Wavesurfer 软件进行分析。配置菜单(choose configuration)分析模式为标准, 得到语图, 语图参数设置为：sampling rate 22 kHz, sample size 16 bit; Aanlysis window length 64。斑背大尾莺雄性个体鸣唱的句子之间没有明显的时间间隔, 根据句式结构(synax structures)划分句子(Päckert et al, 2004); 一直在同一个句子、不同的句子或不同个体间的句子中反复出现的一组音素视为一个音节(Tracy & Baker, 1999; Baker et al, 2000)。语图进一步展开得到功率频谱图, 分析选择 FFT(快速傅立叶变换); 窗口选择 Hamming; FFT Point 在预览时选择 512, 最终处理时 FFT Point 选择 1 024。通过语图统计数据：每个句子的音节个数(number of syllables, NS), 每个音节的音素个数(number of notes, NN)。测量参

数包括：句子持续时间(duration of verse, VD)、音节持续时间(duration of syllable, DS)、音节间隔时间(interval of syllable, SI)(图 1)。

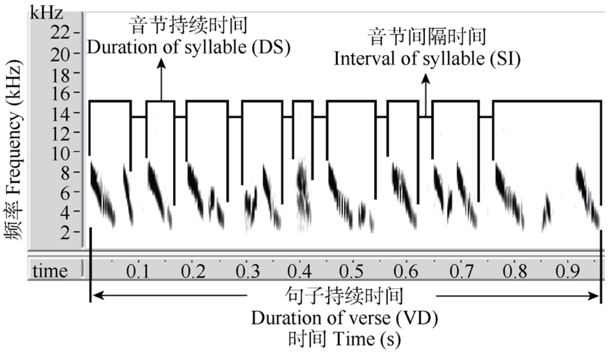

图 1　参数测量示意图

Fig. 1　Method of measuring the parameters

2.5　鸣声参数分析

利用 spss17.0 软件，首先进行正态分布检验，符合正态分布的采用单因素方差分析(one–way ANOVA)进行差异性检验。文中平均数以 Mean±*SE*(range) 的方式表示。

2.6　前部句子的节奏(rhythm)特征分析

A 句式的前部句子，选取音节个数<16 的 18 个句子，按照句子持续时间递进的顺序，逐个测量每个句子相邻每两个音节的间隔时间，根据音节个数分类，求平均值，做折线图；B 和 C 句式的前部句子，选取音节个数为 16~25(包括 16 和 25)的 12 和 13 个句子，测量每个句子前 5 个音节(FS5)的平均间隔时间，整个句子持续时间中点 5 个音节(MS5)的平均间隔时间，句子最后 5 个音节(LS5)的平均间隔时间，做折线图；D 句式的前部句子不做测量。

3　结　果

斑背大尾莺雄性个体的鸣声，包括鸣叫和鸣唱。根据斑背大尾莺雄性个体行为特征，定义为求偶炫耀鸣唱、报警声和联络声。分析和测量了 20 只斑背大尾莺雄性个体的鸣声，得到 38 种音节型(图 2)。其中，31 种音节至少被两只个体所共享，占音节类型总数的 81.6%；7 种音节仅为某一个体所特有，占音节类型总数的 18.4%；没有一种音节被所有个体共享。

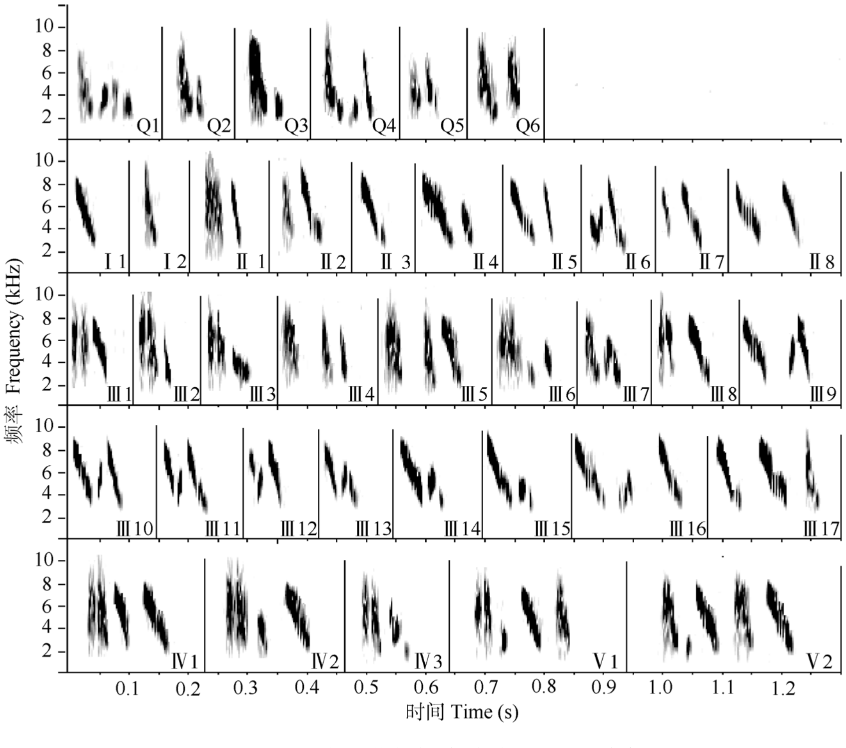

图 2　20 只斑背大尾莺雄性个体鸣声的 38 种音节型

Fig. 2　38 syllable types of Japanese marsh warbler

Q1~Q6 为前部句子的音节型，其中“Q”为“前”的缩写；其余为主体部句子的音节型，其中罗马数字表示组成该音节的音素个数，阿拉伯数字表示序号；Q2 也为报警声音节，Ⅰ2 也为联络声音节。

Q1 − Q6 are the syllables of the first part in the verses, “Q” is the abbr. of the Chinese word “qian”; The syllables of the main part have followed, Roman numerals show the number of notes in the syllables, Arabic numerals shows the ordinal; Q2 is also the syllable type of alarm call, Ⅰ2 is also the syllable type of contact call.

3.1 求偶炫耀鸣唱(courship song)

3.1.1 行为特征 斑背大尾莺在整个繁殖期都会发出求偶炫耀鸣唱。繁殖前期，雄鸟通常停在领域内非常显著的枯芦苇枝或小树枝上，然后飞向空中鸣唱，运动路线呈十分明显的弧线(抛物线状)；鸣唱时，头部在空中不停地左右摆动，鸣唱持续的时间很短，在 10 s 以内；最后落回鸣唱前停留的枯芦苇枝或小树枝上。繁殖后期，飞向空中伴随鸣唱的行为明显减少，只是停在领域内枯芦苇枝或小树枝上鸣唱。鸣唱时，头部仍然不停地左右摆动，鸣唱持续时间仍然在 10 s 以内。

3.1.2 鸣唱特征 斑背大尾莺雄性个体的求偶炫耀鸣唱可分为两类：第一类具有两部分组成，前一个句子由简单的音节(单音节或双音节)不断重复构成(文中简称前部)，后一个句子由复杂的音节构成(文中简称主体部)；第二类由复杂的音节构成一个句子(文中简称主体部)。所录音的 20 只个体中，12 只个体同时具有第一类和第二类鸣唱，8 只个体只具有第一类鸣唱。由于斑背大尾莺雄性个体求偶炫耀鸣唱的“前部”特点突出，所以本文将前部句子和主体部句子分开分析。

3.1.2.1 前部句子句式特征 斑背大尾莺雄性个体求偶炫耀鸣唱的前部句子，是相同音节的不断重复(图3)。12只个体95个鸣唱句子具有音节类型6种(图

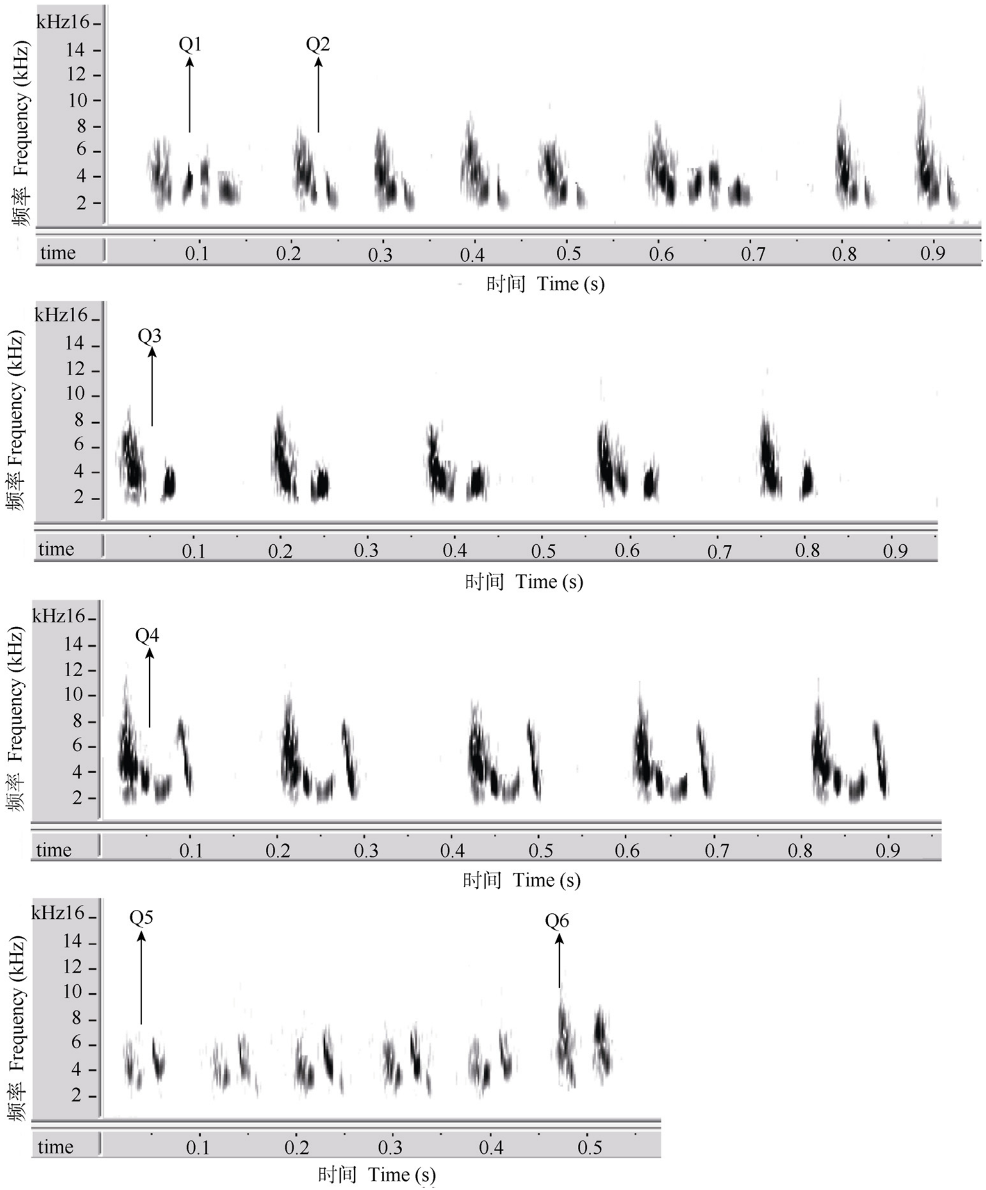

图 3 斑背大尾莺求偶炫耀鸣唱前部句子语图(依次为 A、B、C 和 D 句式)

Fig. 3 Song spectrum of courtship song of Japanese marsh warbler (Synax A, B, C and D in turn)

表 1　斑背大尾莺鸣唱特征参数

Tab. 1　Song characteristics parameters of Japanese marsh warbler

	句式 Synax	样本量 Sample size	测量句子总数 Total number of verses	句子数 Number of verses				句子持续时间 VD(s)	句子音节个数NS	音节持续时间 DS(s)	音节间隔时间 SI(s)
				音节个数 NS <16	音节个数 NS 16~25	音节个数 NS 26~100	音节个数 NS >100				
前部句子 The first part	A	4	34	18	13	3	0	4.573±1.151 0.672~31.782	15.515±1.690 3~50	0.062±0.001 0.041~0.111	0.065±0.004 0.010~0.150
	B	3	29	2	12	11	4	8.017±1.939 0.885~36.297	55.828±13.195 10~275	0.051±0.001 0.040~0.065	0.067±0.007 0.021~0.152
	C	4	31	6	13	9	3	6.418±1.262 1.167~35.473	30.516±5.425 7~139	0.082±0.001 0.075~0.087	0.108±0.008 0.053~0.280
	D	1	1	—				0.522	7	0.045±0.004 0.027~0.054	0.034±0.005 0.011~0.046
主体部句子 Main body part	复杂音节组成	20	501	—				3.958±0.068 1.770~6.195	32.023±0.538 16~45	0.092±0.001 0.023~0.243	0.029±0.001 0.017~0.145

“—”表示未测量(means non-measured)。

2, 第一行), 组成 4 种不同的句式。分别为：A 句式：Q1Q1Q1…Q2Q2Q2…Q1Q2Q2, Q1Q2Q2...Q1Q2Q2; B 句式：Q3…Q3; C 句式：Q4…Q4; D 句式：Q5Q5Q5Q5Q5Q6Q6。

求偶炫耀鸣唱前部句子的参数见表 1。

A 句式音节个数最少, 音节个数<16 的句子数量最多; B 句式音节个数最多, 音节个数 16~25 的句子数量最多; C 句式中, 音节个数 16~25 的句子数量最多; D 句式被一个个体独有。

3.1.2.2　前部句子节奏(rhythm)特征　斑背大尾莺求偶炫耀鸣唱前部句子的音节间隔时间随句子持续时间的延长而逐渐缩短, 即句子节奏逐渐变快(图 4)。

图 4a 显示, 随着句子持续时间的延长音节间隔时间逐渐缩短; 图 4b、4c 显示, FS5>MS5>LS5, 即随着句子持续时间的延长音节间隔时间逐渐缩短。

3.1.2.3　主体部句子特征　共测量了 20 只斑背大尾莺雄性个体 501 个鸣唱句子(图 5a), 得到 32 种音节类型(图 2, 第二行到最后一行)。平均每个个体鸣唱句子个数为 25.05 个。其中组成音节的音素最少为 1 个, 最多为 5 个。参数见表 1。

3.1.3　个体鸣唱差异　20 只斑背大尾莺雄性个体求偶炫耀鸣唱的 4 个参数均符合正态分布, 所以采用单因素方差分析(one–way ANOVA)法进行差异性检验。检验结果显示, 斑背大尾莺求偶炫耀鸣唱的 4 个参数：句子持续时间(F =7.727, P<0.01)、句子音节个数(F=3.324, P<0.01)、音节持续时间(F=23.761, P<0.01)、音节间隔时间(F=2.742, P<0.01)均差异极显著。

3.2　报警声(alarm call)

在人为干扰情况下, 人与斑背大尾莺个体距离在 10 m 以内时, 斑背大尾莺个体就会发出急促、响

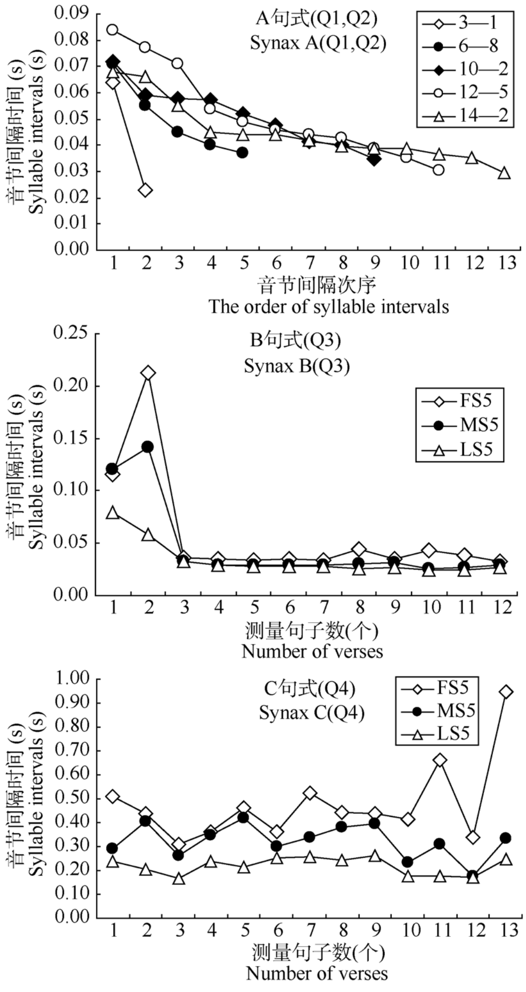

图 4　斑背大尾莺前部句子节奏特征(依次为 A、B 和 C 句式)

Fig.4　Rhythm characteristics of the first part verses of Japanese marsh warbler (Synax A, B and C in turn)

4a 图例中, 前面数字表示音节数, 后面数字表示句子数(如 “3-1”, 表示由 3 个音节组成的 1 个句子被测量)。

4b 和 4c 图例中的 FS5、MS5、LS5 含义已在前文方法中说明(见 2.6 节)。

In fold-line graph of 4-a, the front numerals of the legend show the number of syllables, latter numerals show the number of verses which were measured (For example, “3-1” means one verse was measured which has 3 syllables).

In fold-line graph of 4-b and 4-c, the meaning of FS5, MS5 and LS5 have already mentioned in Methods which in the front of this thesis (Methods 2.6).

亮的报警声，持续时间较长，但并不隐蔽。而当人处于某一固定位置，距离大于 10 m，且不活动时，斑背大尾莺个体就不会再发出报警声了。非同种的其他鸟在空中飞过时(高度约 50 m)(如鹊鹞、苍鹭、黑嘴鸥)，斑背大尾莺个体也发出急促的报警声，持续时间较短，然后随即隐藏到草丛中，消失不见。以上两种情况，当一只个体开始发出报警声后，附近 30 m 范围内的其他个体也随之发出报警声。

报警声为音节 Q2 的快速重复(图 5b)；持续时间最短为 0.540 s，最长为 4.268 s；音节个数最多 56 个，最少 5 个。参数见表 2。

3.3 联络声(contact call)

斑背大尾莺雄性个体在枯树枝或芦苇枝上发出联络声时，随即雌性个体也会发出应答。以下分析的是雄性个体的联络声。

联络声为 I 2 音节型的不断重复(图 5c)；持续时间较长，最长可达 119.021 s，最短为 5.763 s；音节个数最多 554 个，最少 23 个。参数见表 2。

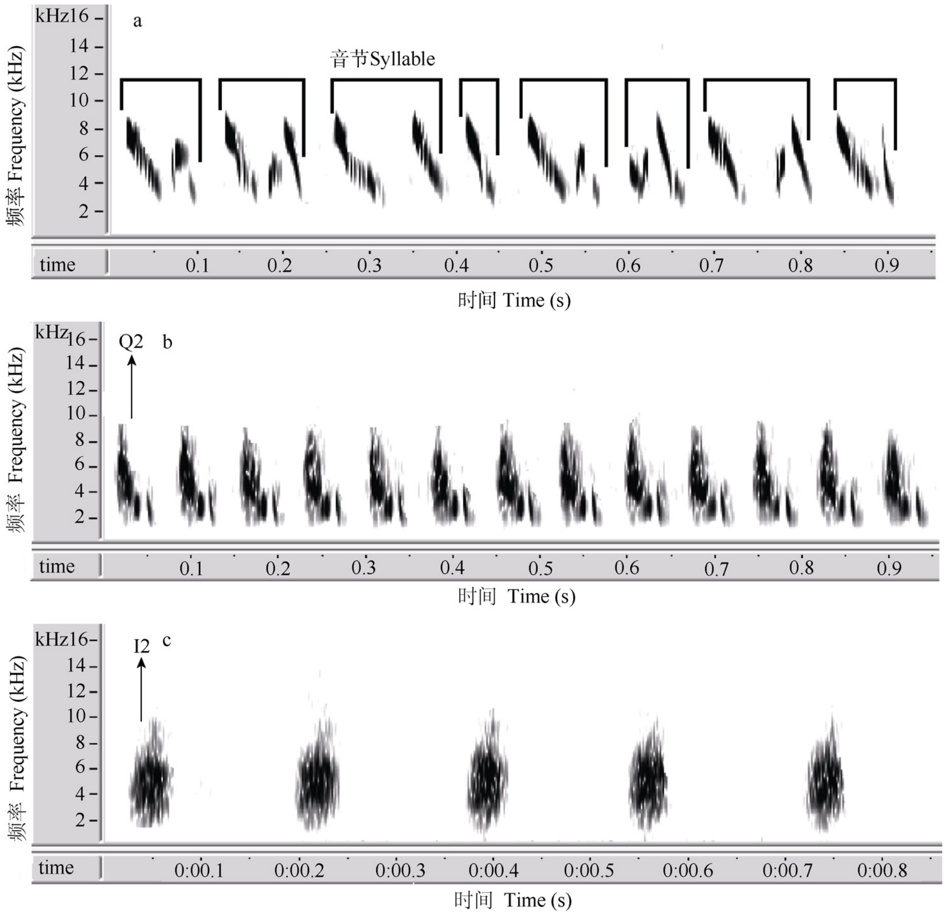

图 5 斑背大尾莺求偶炫耀鸣唱语图(句子的一部分)(a)、报警声语图(b)和联络声语图(c)

Fig. 5 Song spectrum of courtship song of Japanese marsh warbler (one part of the verses)(a), spectrum of alarm call (b), and Spectrum of contact call (c)

表 2 斑背大尾莺雄性个体报警声和联络声特征

Tab. 2 Parameters of alarm call and contact call of Japanese marsh warbler

	样本量 Sample size	测量句子数 Number of verses	句子持续时间 VD(s)	句子音节个数 NS	音节持续时间 DS(s)	音节间隔时间 SI(s)
报警声 Alarm call	9	35	1.746±0.193 0.540~4.268	23.086±2.472 5~56	0.047±0.000 0.021~0.069	0.026±0.000 0.011~0.039
联络声 Contact call	2	7	32.485±14.672 5.763~119.021	155.286±67.99 423~554	0.040±0.000 0.027~0.047	0.187±0.008 0.092~0.642

由于样本数过小，没有对报警声和联络声各项参数进行差异性检验。

One-way ANOVA was never be used for the Alarm call and contact call because of the sample size is small.

4 讨 论

Szekely et al(1996)比较了蝗莺属黑斑蝗莺(*Locustella naevia*)、鸲蝗莺(*Locustella luscinioides*)以及苇莺属芦莺(*Acrocephalus scirpaceus*)、蒲苇莺(*Acrocephalus schoenobaenus*)、大苇莺(*Acrocephalus arundinaceus*)等的鸣唱特征，发现蝗莺属鸟类的鸣唱是所有鸣禽中鸣唱最简单的，由单音节或双音节的不断重复组成；而苇莺属鸟类的鸣声复杂，雄性个体鸣声的音节类型数量可能达到百种。目前，许多研究认为斑背大尾莺在分类地位上与蝗莺属鸟类更接近(Zhang, 2007)，且已有一些研究已将斑背大尾莺由大尾莺属划分到蝗莺属(Mackinnon et al, 2000)。在鸣声方面，斑背大尾莺鸣声的复杂程度比蝗莺属复杂很多，相差较远，与苇莺属鸟类很接近。

组成斑背大尾莺雄性个体鸣声的音素，根据在鸣声句子中出现和排列顺序的不同，可以被组合成许多不同的音节类型，同一个音素可以在多个音节类型中出现。求偶炫耀鸣唱由两个句子构成，在音节组成和句子节奏上，前部句子由节奏不断加快的简单的单音节(Q3, Q4)或双音节(Q1, Q2, Q5, Q6)重复组成；主体部句子由复杂的音节按照特定的排列顺序组成，句子节奏稳定，音节平均间隔时间均短于4种前部句子。在句子持续时间上，除由音节Q5、Q6组成的第四种前部句子外，其他3种前部句子的平均持续时间都长于后面主体部句子的平均持续时间。苇莺属鸟类蒲苇莺(*Acrocephalus schoenobaenus*)鸣声音节的构成方式与斑背大尾莺类似；鸣声句子的开始部分和中间部分也和斑背大尾莺具有类似的特征(Buchanan & Catchpole, 1997; Catchpole, 2000)。蒲苇莺鸣声句子开始部分的持续时间很长，由两个持续时间较短的音节交替出现；然后迅速转变成更大声，更快的中间部分；句子最后部分的形式与开始部分一样，而音节出自句子的中间部分(Catchpole & Slater, 2008)。斑背大尾莺求偶炫耀鸣声只有两部分句子，没有第三部分，与蒲苇莺相比，相对简单。

许多苇莺属的鸟类，领域防御鸣声简单，求偶炫耀鸣声复杂(Catchpole, 2000)。斑背大尾莺雄性个体的鸣声亦符合这个特征。组成求偶炫耀鸣唱前部句子的音节个数变化范围很大，从3~275个。在所录的20只斑背大尾莺个体中，只有12只个体的求偶炫耀鸣唱具有前部句子，每只个体只有一种类型的前部句子，没有两只个体的前部句子是完全相同的。对求偶炫耀鸣唱主体部句子的参数比较发现，在句子的音节组成数量和时间上都存在极显著的个体差异。在句型上也各不相同，平均一个个体有至少4种句型，不同个体之间没有发现相同的句型。

报警声句子由单音节(Q2)构成一种简单句型，句子节奏最快，声音最大。声音信号是与邻居保持联系最明显的一种方式，并且它能够促使种内个体聚集(Forsman & Mönkkönen, 2001)。而报警声就是其中之一，是许多物种在面对即将发生的危险时发出的特定的声音信号(Caro, 2005)，通常提醒种群内的成员对捕食者的潜在威胁开始警戒(Seyfarth et al, 1980)。

根据不同的作用，报警声可以分为许多种类，如警报提示声(alerting call)、防御声(defense call)、攻击声(attack call)、聚众集群声(hawk and mobbing call)、吸引捕食者叫声(predator attraction)、追踪威慑声(pursuit-deterrent call)、遇险求救声(distress call)、警戒守卫声(on-guard call)和干扰声(distraction call)等(Placer & Slobodchikoff, 2004)。鸣叫声的结构复杂程度取决于叫声的作用。多重作用，鸣叫声的结构也复杂；作用单一，鸣叫声结构也简单(Marler, 2004; Kaplan, 2008)。斑背大尾莺利用报警声对危险信号进行传递，通知种群内其他成员隐蔽；没有发起攻击也没有集群；句子结构简单。根据这些特点，判断此类报警声为相对简单的一种，即警报提示声(alerting call)。

联络声是动物联络通讯的重要信号，包括雌雄个体之间的联络声，亲鸟和雏鸟之间的联络声，种群个体之间的相互联络(Cortopassi & Bradbury, 2006)。联络声中包含着鸣叫者的身份和种群从属关系方面的信息，作用多样。一些鸟类配偶之间交流时，雄性个体可以更多的模仿配偶的叫声；而此雄性个体与未知的或不熟悉的其他雌性个体交流时不会表现出这种特征(Striedter et al, 2003)。联络声作用复杂，结构特征也变化多样(Cortopassi & Bradbury, 2006)。斑背大尾莺雄性个体的联络声由单音节的不断重复组成句子，句子的音节组成数量和持续时间变化范围很大。在研究区域内，进行斑背大尾莺雄性个体联络声回放实验发现，至少会有一只雌性个体出现，在声源附近的草丛中钻进钻出，多数情况下会发出鸣叫声回应。另外，在几处巢附近，记录到配偶之间利用此联络声交流。据目前的

行为观察和回放实验，仅能判断此联络声存在于雌雄个体之间，而是否也存在于亲鸟和雏鸟之间或种群内其他成员之间还有待于更深入研究。

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云南纳帕海越冬黑颈鹤夜栖地特征

BACK

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摘要：2009 年 11 月至 2010 年 4 月对云南省香格里拉县纳帕海省级自然保护区越冬黑颈鹤(*Grus nigricollis*)的夜栖地的特征进行了调查。采用三角定位标图结合标志物校正法确定夜栖地方位，并进行实地校正。共记录夜栖地 63 个，均位于有水的斑块状沼泽中，基底大多有泥层，大部分(81.0%)有植被覆盖。夜栖地与人类活动区域和沼泽岸边有一定距离。与随机对照样地相比，夜栖地基底泥层较厚(Z=−2.365, P=0.018)，明水面比例较大(Z=−3.086, P=0.002)，离道路、村庄和农田较远(Z/t=−2.852～−2.334, P=0.008～0.020)，水深在两者间有极显著差异(χ^2=16.730, P=0.001)。夜栖地利用前后对比发现沼泽斑块的面积有显著差异(t=2.977, P=0.021)。主成分分析表明影响黑颈鹤夜栖地利用的因素依次为人类干扰、沼泽斑块大小和浅水环境状况。

关键词：黑颈鹤; 夜栖地特征; 纳帕海
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Roosting-site characteristics of wintering black-necked cranes (*Grus nigricollis*) at Napahai, Yunnan

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Abstract: From November 2009 to April 2010, roosting-site characteristics of black-necked cranes (*Grus nigricollis*) were observed at Napahai Provincial Nature Reserve, Shangri-La, Yunnan, China. The positions of roosting-sites were determined by triangulation with markers and field correction. All of the 63 roosting-sites observed were located in patchy marshes with water, which contained some mud on the bottom and 81% of the roosting-sites were covered by plants. They also had a certain distance to areas of human activities and had a certain distance to the shore. A comparison of roosting sites and random sites showed that roosting-sites had thicker mud layers, a higher ratio of open water, longer distance to roads, villages, and farmland, and water depth. Another comparison of before and after usage of roosting-sites found a significant difference in area of marsh patch. Principal component analysis indicated that the usage of roosting-site of black-necked cranes was affected by human disturbance, area of marsh patch, and the condition of the shallow water environment.

Key words: Black-necked crane; Roosting-site characteristics; Napahai

栖息地是动物赖以生存的环境，而夜栖地是动物夜间利用的场所，是栖息地的重要组成部分。昼行性鸟类在夜晚往往处于被动和不利的环境，因而夜栖地的质量在一定程度上关系到它们在夜间的安全(Engel & Young, 1992)。对一些珍稀濒危雉类的研究发现，夜栖的环境质量能影响其生存和繁殖(Lu & Zheng, 2002; Jang et al, 2006; Kang & Zheng, 2007)。对沙丘鹤(*Grus canadensis*)的研究表明，它会选择远离河道或湿地岸边的浅水区域作为夜栖地(Krapu et al, 1984; Folk & Tacha, 1990)。

黑颈鹤(*Grus nigricollis*)是世界上惟一一种主要分布在中国的鹤类，也是惟一一种终生生活在高

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原的鹤类(Li & Li, 2005), 属国家 I 级重点保护野生动物。目前有关其栖息地的研究大多以日间栖息地为研究对象(Tsamchu & Mary, 2005; Liu, 2007; Kong et al, 2008; Zhao et al, 2008; Liu et al, 2010); 而对夜栖地的研究仅见于 Bishop et al(1998)对西藏越冬黑颈鹤栖息地的观察和 Liu et al(2008)在纳帕海对越冬黑颈鹤集群特征的分析, 以及 Li & Li(2005)对过去有关黑颈鹤夜栖地定性描述的总结。目前, 还未见有关黑颈鹤夜栖地之特征的定量分析研究。鉴于此, 笔者在纳帕海对越冬黑颈鹤的夜栖地的特征进行了调查, 并对影响其夜栖地利用的相关因素进行了探讨。

1　研究地点和方法

1.1　研究地区概况

云南纳帕海省级自然保护区(N27°47’58”~27°55’00”, E99°35’43”~99°40’56”)位于云南省迪庆藏族自治州香格里拉县(原中甸县)境内, 总面积为 3 435 hm^2(Zhao et al, 2008)。保护区在海拔 3 260～3 300 m 之间, 具有高寒、霜期长、降水少、冬春干旱和冬季漫长而寒冷等气候特点(Mu, 2007; Li & Yang, 2005; Liu et al, 2008; Wang et al, 2009)。纳帕海由周围四条河流供水, 冬季湖水从保护区北部山脚下的天然落水洞排出, 从而使保护区成为浅水沼泽, 为许多越冬水鸟提供了良好的栖息环境(Li & Yang, 2005; Liu et al, 2007), 同时也成为黑颈鹤中部种群的主要越冬地(Li, 2005)。

1.2　研究方法

1.2.1　调查方法　2009 年 10 月下旬在黑颈鹤迁来越冬时开展预调查, 了解黑颈鹤的夜栖地分布和变化情况, 并确定观察地点、调查方法和需收集的生境变量信息。2009 年 11 月 27 日至 2010 年 4 月 29 日正式调查, 除 11 月外, 每月对黑颈鹤的夜栖地进行至少 2 次(2~4 次)调查, 两次调查间隔在 1~2 周之间。在多雾、阴雨雪等影响观察和不能准确确定夜栖地位置的天气不作观察, 每月实际调查次数分别为 11 月 1 次、12 月 2 次, 以及翌年 1 月 2 次、2 月 4 次、3 月 3 次、4 月 4 次, 共调查 16 次。

根据预调查结果, 在纳帕海周围山腰和两个观鸟台共设置 7 个观察点, 每次调查时根据前一次夜栖地的分布情况选取 2~4 个观察范围可覆盖整个保护区的观察点进行观察, 保证每次调查皆可覆盖保护区内所有黑颈鹤夜栖地。调查时间为黑颈鹤飞离夜栖地之前的上午 6:30~8:30。在观察点用单筒望远镜(Carl Zeiss, Disacope 85 T×FL, 20~60 mm×85 mm)顺时针扫描整个保护区内的夜栖地, 采用三角定位标图结合标志物校正法在 1:30 000 的地图上确定黑颈鹤夜栖地 GPS 位点, 并标出夜栖地所在沼泽斑块的边缘。调查中将群体大小≥5, 与其他夜栖群的边缘距离≥300 m, 且连续利用时间大于 10 d 的夜栖地作为独立的取样单位。

根据所记录的夜栖地 GPS 位点并结合实地黑颈鹤的利用痕迹, 核对其实际的夜栖地。经实地调查, 标图法确定的夜栖地与实际利用的夜栖地点距离相差 100~200 m, 小于本研究定义的夜栖地间距离(300 m)。实地记录夜栖地的水深、明水面比例、泥层厚度、植被类型、植被盖度与高度。通过地图软件 Global Mapper 10(Global Mapper LLC, 2009)测量距岸边的距离(为夜栖地边缘距离岸边的最近距离)、夜栖地离道路、村庄、农田和河道的距离等变量以及夜栖地所在沼泽斑块的面积, 泥层厚度由调查者静立于夜栖地时陷入的深度来测量。

1.2.2　分析方法　为了探讨影响纳帕海黑颈鹤夜栖地利用的因素, 共设计了两种对照地：在前期(2009 年 12 月)设置随机对照地(利用−不利用对照)以得出黑颈鹤夜栖地的特殊生境特征; 在后期(2010 年 2~4 月)设置利用后对照地(利用−放弃对照)来找出使之放弃该夜栖地的因素。随机对照地通过在 300 m×300 m 的网格中随机选取, 以网格中心为对照地点, 共选取 16 个对照地。利用后对照地为黑颈鹤放弃后的夜栖地, 共有 8 处。

1.3　数据处理

将所有夜栖地及两种对照地的特征数据输入计算机, 用统计软件 PASW Statistics 18 进行统计分析。在比较均值前, 先对数据进行 Kolmogorov-Smirnov 正态性检验, 符合正态分布的数据用 *t* 检验, 不符合正态分布的数据用 Mann-Whitney *U* 检验。夜栖地与随机对照地作为两个独立样本进行比较, 而夜栖地利用前后对照作为配对样本进行比较。为了不遗漏某些数据分布不同但未能从均值上反映出差异的变量, 对各变量的数据进行分类处理, 用列联表进行分析, 并进行卡方检验。

主成分分析是为了将影响纳帕海黑颈鹤夜栖地利用的较多因素归类为几组因子, 每组因子内的因素间相关性较高, 不同因子间相关性低, 以利于综合分析影响夜栖地利用的因素。将利用−不利用

比较和利用−放弃比较后得出的差异显著的变量作为影响黑颈鹤对于夜栖地利用的主要变量, 以所发现的 63 处的夜栖地为样本进行主成分分析。主成分分析时, 在得出因子载荷矩阵后进行正交旋转, 使各因子分离明显。

2 结 果

2.1 夜栖地特征

2009 年 11 月至 2010 年 4 月共发现夜栖地 63 个, 每次调查平均有(3.9±0.4)个(1~6 个, n=16)。这 63 处的夜栖地全都位于浅水沼泽, 96.8%(61 处)的夜栖地基底都有泥层覆盖。夜栖地中的植被类型主要有挺水植物、浮水植物、挺水与浮水植物并存、无植物等 4 类, 数量及比例分别为 36(57.1%)、11(17.5%)、4(6.3%)、12(19.0%), 具有各类植物的夜栖地共计有 51 处, 占 81.0%。这 63 处的夜栖地的生境特征见表 1。

从表 1 可知, 纳帕海越冬黑颈鹤的夜栖地均分布在有水的斑块状沼泽区域中, 与岸边有一定距离, 水深小于 30 cm, 基底大多有泥层分布, 大部分有一定植被覆盖, 与人类活动区域(道路、村庄、农田)有一定距离。

2.2 夜栖地与随机对照地的比较

将 2009 年 11~12 月记录的 15 个夜栖地与 2009 年 12 月选择的 16 个对照地的生境变量做对比。结果发现, 前者的基底泥层较厚($Z=-2.365$, $P=0.018$), 明水面比例较高($Z=-3.086$, $P=0.002$), 距道路、村庄和农田的距离较大($Z/t=-2.852$～-2.334, $P=0.008$～0.020)。而水深、植被盖度、植被高度、距河道的距离则无显著差异($Z/t=-1.521$～0.934, $p=0.128$～0.919)(表 2)。对这些变量的数据分布状况进行分析后, 发现水深在夜栖地与随机对照地两者间有所不同(图 1)。卡方检验发现两者间有极显著差异($\chi^2=16.730$, $df=3$, $P=0.001$), 其他变量的数据分布无差异($\chi^2=0.322$～5.526, $P=0.137$～0.851)。

表 1 纳帕海越冬黑颈鹤夜栖地生境特征描述统计

Tab. 1 Descriptive statistics of roosting-site characteristics of wintering Black-necked Cranes at Napahaik, Yunnan, China

生境变量 Variable	均值 Mean	标准差 *SD*	范围 Range
沼泽面积 Area of marsh patch (hm^2)	19.4	20.6	0.8~106.5
水深 Water depth (cm)	8.3	5.1	2.8~27.2
泥层厚度 Mud thickness (cm)	21.6	18.6	0~53.0
植被盖度 Vegetation cover (%)	50	35	0~100
植被高度 Vegetation height (cm)	12.8	15.9	0~50.0
明水面比例 Ratio of open water (%)	82	16	50~100
距岸边距离 Distance to shore (m)	141	93	6~465
距道路距离 Distance to road (m)	540	203	160~1100
距村庄距离 Distance to village (m)	974	295	580~1700
距农田距离 Distance to farmland (m)	991	373	350~1700
距河道距离 Distance to river (m)	573	422	95~1550

表 2 纳帕海越冬黑颈鹤夜栖地与随机对照地生境变量的比较

Tab. 2 Comparison of habitat variables between roost sites and random sites of wintering Black-necked Cranes at Napahai, Yunnan, China

生境变量 Variable	统计值 Statistic(Mean±*SE*)		检验 Test		P
	夜栖地 (n=15) Roost site	对照地 (n=16) Random site	t^{a}	Z^{b}	
沼泽面积 Area of marsh patch (hm^2)	16.5±6.7				
水深 Water depth (cm)	14.3±1.6	17.7±7.4		−1.521	0.128
泥层厚度 Mud thickness (cm)	19.7±5.7	12.6±7.1		−2.365	**0.018***
植被盖度 Vegetation cover (%)	60±9	66±10		−0.602	0.547
植被高度 Vegetation height (cm)	9.1±3.3	7.3±2.3		−0.101	0.919
明水面比例 Ratio of open water (%)	92±4	36±12		−3.086	**0.002****
距岸边距离 Distance to shore (m)	135±34				
距道路距离 Distance to road (m)	652±64	382±107		−2.334	**0.020***
距村庄距离 Distance to village (m)	1207±94	797±108	−2.852		**0.008****
距农田距离 Distance to farmland (m)	1135±102	669±136	−2.711		**0.011***
距河道距离 Distance to river (m)	482±86	625±124	0.934		0.358

^{a} 独立样本 t 检验, t 值; ^{b} 独立样本 Mann-Whitney U 检验, Z 值; $^{*}P<0.05$; $^{**}P<0.01$。

^{a} Independent-Samples t test, t value; ^{b} Independent-Samples Mann-Whitney U test, Z value.

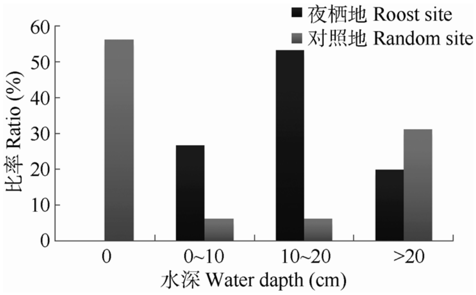

图 1　纳帕海越冬黑颈鹤夜栖地与对照地水深的比较

Fig. 1　Comparison of Water dapth between roost sites and random sites of wintering Black-necked Cranes at Napahai, Yunnan, China

2.3　夜栖地利用前后的比较

将 2010 年 2—4 月间记录的 8 组黑颈鹤利用前后夜栖地的生境变量做对比。结果发现只有沼泽斑块的面积显著减小(t=2.977, P=0.021), 其余均无显著差异(Z/t=−2.007～1.319, P=0.085～1.000)(表 3)。对利用前后两者的数据分布进一步分析后, 也未发现有显著差异(χ^2=0.000～2.286, P=0.131～1.000)。

2.4　夜栖地生境变量的主成分分析

提取以上两种比较中差异显著的生境变量进行主成分分析(表4)。前3个因子的特征值大于1, 故将这 3 个因子作为主成分, 其累积贡献率达到 71.7%。从这 3 个主成分在 7 个变量上的因子负荷可知, 第一主成分主要与夜栖地基底泥层厚度和夜栖地距道路、村庄、农田的距离相关, 主要反映安全和人类干扰情况; 第二主成分主要与夜栖地所在沼泽斑块的面积相关; 第三主成分主要与水深和明水面比例相关, 为浅水环境状况。

表 3　纳帕海越冬黑颈鹤夜栖地利用前后生境变量的比较

Tab. 3　Comparison of roosting-sites habitat variables between before and after usage of wintering Black-necked Cranes at Napahai, Yunnan, China

生境变量 Variable	统计值 Statistic(Mean±SE)		检验 Test		P
	利用前(n=8)Before	利用后(n=8)After	t^{a}	Z^{b}	
沼泽面积 Area of marsh patch (hm^2)	19.6±4.3	10.3±3.1	2.977		**0.021***
水深 Water depth (cm)	6.6±1.2	4.6±0.9	1.319		0.229
泥层厚度 Mud thickness (cm)	17.9±5.8	21.6±5.6	−2.007		0.085
植被盖度 Vegetation cover (%)	24.0±9	31.0±14		−1.342	0.180
植被高度 Vegetation height (cm)	6.9±4.3	8.1±5.0		−1.414	0.157
明水面比例 Ratio of open water (%)	78.0±6	76.0±8	0.454		0.664
距道路距离 Distance to road (m)	539.0±80	539.0±80		0.000	1.000
距村庄距离 Distance to village (m)	924.0±111	953.0±108	−1.000		0.351
距农田距离 Distance to farmland (m)	934.0±111	924.0±118	1.000		0.351
距河道距离 Distance to river −(m)	549±182	531±168		−0.447	0.655

^{a}配对样本 t 检验, t 值; ^{b}配对样本 Mann-Whitney U 检验, Z 值; $^{*}P$<0.05。

^{a} Paired-Samples t test, t value; ^{b} Paired-Samples Mann-Whitney U test, Z value.

表 4　纳帕海越冬黑颈鹤夜栖地生境变量的主成分分析

Tab. 4　Principal component analysis of roosting-site habitat variable of wintering Black-necked Cranes at Napahaik, Yunnan, China

生境变量 Variable	主成分 Component		
	1	2	3
泥层厚度 Mud thickness (cm)	**−0.613**	−0.426	0.352
距道路距离 Distance to road (m)	**0.837**	−0.277	−0.037
距村庄距离 Distance to village (m)	**0.763**	0.262	−0.180
距农田距离 Distance to farmland (m)	**0.797**	-0.259	−0.018
沼泽面积 Area of marsh patch (hm^2)	−0.264	**0.770**	−0.423
水深 Water depth (cm)	0.445	0.339	**0.539**
明水面比例 Ratio of open water (%)	0.065	0.450	**0.723**
特征值 Eigen value	2.564	1.304	1.151
贡献率 Variance explained (%)	36.635	18.631	16.436
累积贡献率 Cumulative (%)	36.635	55.266	71.702

n=63; 粗体表示因子负荷的绝对值>0.5。

Bold numbers indicate absolute values of factor load >0.5.

3　讨　论

研究结果显示, 纳帕海越冬黑颈鹤通常选择有水的斑块状沼泽作为夜栖地点。这些地方水深小于 30 cm, 底层大多有泥层分布, 有一定的植被覆盖, 与人类活动区域(道路、村庄、农田)和岸边有一定距离。这与黑颈鹤在贵州草海夜栖于湖湾的浅水地带(Li, 2005; Li & Li, 2005)、在云南大山包夜栖于水库边(Li et al, 2005)的观察结果相似, 但与西藏越冬的黑颈鹤多在雅鲁藏布江和拉萨河主要支流和水库边缘的浅滩过夜(Li, 2005; Li & Li, 2005; Tsamchu & Mary, 2005)略有差异。这可能与各自所处的地理环境有关。在西藏越冬的黑颈鹤主要在雅鲁藏布江及其支流年楚河、拉萨河的流域, 湖泊湿地较少, 因而仅有的宽阔河流中的浅水区域和水库边就成为合适的夜栖地。

江苏盐城自然保护区越冬的丹顶鹤(*Grus japonensis*)在人工湿地中夜栖(Lü, 2007), 江西鄱阳湖越冬的白鹤(*G. leucogeranus*)夜栖于水面宽大的湖中浅水区(Wu, 2005), 而在西班牙越冬的灰鹤(*G. grus*)夜栖于河流、池塘、和水库中(Avilés, 2004), 这与越冬于云贵高原的黑颈鹤类似; 春季迁徙途经美国中部的沙丘鹤(*G. canadensis*), 其中途停歇的夜栖地既有河道也有湿地(Folk & Tacha, 1990), 与越冬于西藏的黑颈鹤相似。不同鹤类夜栖地生境间的差别可能是适应各自不同生存环境的结果。

3.1 夜栖地对水的依赖

尽管黑颈鹤在白天觅食时并不全都在有水的地方(Liu, 2007; Kong, 2008; Wang, 2008; Li & Li, 2005), 但在夜栖时对水却非常依赖(Li & Li, 2005)。以往的研究认为, 纳帕海越冬黑颈鹤利用湖缘或溪流汇合处, 水深在 10 cm 以上的浅水地带作为其夜栖地(Liu et al, 2008)。此次调查所发现 63 处的夜栖地均位于浅水沼泽中, 水深在 2.8～27.2 cm 之间。主成分分析也将有关浅水环境的水深和明水面比例这两个变量归入影响夜栖地利用的第三主成分(表 4)。可见纳帕海越冬黑颈鹤夜栖时对水的非常依赖。这与云南大山包、贵州草海、西藏越冬黑颈鹤在湖泊和水库边缘、河流浅滩夜栖的观察结果相似(Li, 2005; Li & Li, 2005; Tsamchu & Mary, 2005), 也与丹顶鹤(Lü, 2007)、白鹤(Wu, 2005)、灰鹤(Avilés, 2004)和沙丘鹤(Folk & Tacha, 1990)的研究结果相似。

3.2 夜栖地与觅食地

越冬黑颈鹤白天的觅食地距离夜栖地较近(Kong, 2008), 甚至某些夜栖地也是部分个体白天的觅食地(Zhou et al, 1980)。此次调查中也发现少量黑颈鹤早晨并不是飞离夜栖地, 而是在夜栖地点附近活动、觅食, 逐渐远离夜栖地。所以, 食物可能也是影响黑颈鹤对夜栖地利用的因素之一。黑颈鹤在越冬期主要以植物性食物(Li & Li, 2005)为主, 因而作为觅食地的夜栖地中一般分布有一定的植被。此次调查发现大部分(81.0%)夜栖地中都有植物, 但与随机对照地植被盖度与高度的比较并未发现显著差异。这可能因为鱼类也是纳帕海越冬黑颈鹤的一种重要食物来源(Wang, 2008)。特别是在 3—5 月, 水域非常小, 鱼类集中, 大部分黑颈鹤都到纳帕海北部水域边缘捕食鱼类, 同时夜栖于此。而此地通常很少有植被分布, 因此减小了夜栖地与对照地植被分布的差异。

越冬黑颈鹤日间最偏好的生境在大山包和纳帕海为浅水水域或沼泽(Kong, 2008; Liu, 2007; Wang, 2008; Zhao et al, 2008; Liu et al, 2010); 在草海为莎草草甸(Li, 1999); 而在西藏则为耕地(Bishop & Li, 2002; Li & Li, 2005; Tsamchu & Mary, 2005)。虽然, 这四个地点越冬黑颈鹤的日间栖息地或觅食地有所不同, 但是, 夜栖地却无一例外地选择浅水环境。这可能是因白天和夜晚对环境的需求不同所造成。越冬黑颈鹤日间主要行为为觅食(Kong et al, 2008; Zhao et al, 2008; Wong et al, 2009), 食物是选择生境的主要因素, 因而选择食物较为丰富的地区活动; 夜间一般休息, 食物成为次要因素, 而安全因素则更加重要。

3.3 安全因素

与随机对照地相比, 黑颈鹤的夜栖地明显远离人类活动频繁的地区, 如人们居住的村庄、放牧活动经过的道路和有农业活动的农田; 主成分分析也将泥层厚度和夜栖地距道路、村庄、农田的距离列为第一主成分(表 4)。对沙丘鹤的研究也发现, 夜栖在有桥梁或道路的河流片段鹤的平均数量要比没有人类干扰的河流片段的数量少一半多, 而紧邻桥梁和道路一般为人类活动频繁的地区。这说明人类干扰对沙丘鹤去利用河道产生了极为负面的影响(Krapu et al, 1984), 同时鹤也避免选择窄的河道作为夜栖地(Krapu et al, 1984; Tierny et al, 2001), 白鹤则一般利用无干扰的浅水区域夜栖, 而避开了有干扰的小湖、有渔船和鱼网的大湖(Wu, 2005)。

这些变量在一定程度上反映了夜栖地的安全因素。对一些雉类的研究发现, 安全因素在其夜栖生境中首先被考虑, 因为许多猛禽和野兽都能对它们构成威胁(Jiang et al, 2006; Kang & Zheng, 2007), 并且夜间被捕食的风险更大(Lu & Zheng, 2002)。黑颈鹤在纳帕海是体型最大的鸟类之一, 目前尚未观察到对其具威胁性的猛禽或野兽。由于宗教信仰问题, 当地居民不会对黑颈鹤造成直接伤害, 但常常观察到黑颈鹤会对接近的人发出警戒鸣叫, 甚至飞走。所以, 人类活动的间接干扰, 如放牧、捡牛粪、家狗等, 可能是影响黑颈鹤选择夜栖地的最主要因素。然而, 纳帕海地势平坦, 黑颈鹤很容易被人类和其他动物发现。因此, 它们就必须选择远离这些干扰的合适生境作为夜栖地。纳帕海的生境类型主要有开阔水域、浅水沼泽、草地和耕地等(Liu, 2007;

Wang, 2008)，其中草地是人和其他动物可以直接进入的；开阔水域中水较深，不适合站立，黑颈鹤白天也很少在其中活动(Liu, 2007; Wang, 2008)；只有浅水沼泽较为远离道路、村庄和农田，是人类间接干扰难以到达的区域，因而成为黑颈鹤理想的夜栖场所。对沙丘鹤的研究也发现，在河道和季节性湿地中的夜栖地都位于浅水区域(Folk & Tacha, 1990)，河道和湿地的状况影响了沙丘鹤的分布(Krapu et al, 1984; Folk & Tacha, 1990)。

但并不是任何浅水沼泽都适合作为夜栖地。某些沼泽呈网状分布，其间夹杂有块状或网状的草地，并不能阻止人和其他动物进入；某些沼泽面积较小，也能够接近。因此，黑颈鹤只利用那些面积较大(>0.8 hm^2)、水面较多(>40%)的沼泽斑块进行夜栖。夜栖地利用前后对比也发现，当水位下降、沼泽斑块面积缩小时，黑颈鹤就会放弃此夜栖地。同时，黑颈鹤一般站立于沼泽斑块的中央，离岸边有一定距离，这可能是减少直接干扰的对策，因为这一距离可以使黑颈鹤及早发现入侵者。对沙丘鹤的研究也发现，夜栖的位置离岸边距离这个生境变量相当重要：鹤将远离岸边的地方作为夜栖地，并且缺乏水形成的屏障就不能成为安全的夜栖生境(Krapu et al, 1984)，而对其他变量则要求没那么严格(Folk & Tacha, 1990)。

大面积的浅水沼泽斑块能够阻挡人类干扰的另一个重要原因是基底有泥层分布。此次调查中绝大部分(96.8%)夜栖地均有泥层，有些厚度甚至达到 50 cm 以上。这虽然增加了实地调查的困难，但也说明泥层可以有效地阻止人类或其他动物的进入。

3.4　其他影响因素

在对黑颈鹤夜栖地利用前后的生境变量比较后，发现只有沼泽面积有显著减小，说明沼泽斑块的大小变化对纳帕海越冬黑颈鹤的夜栖地利用非常重要：当其减小到一定程度时，黑颈鹤就会放弃对此夜栖地的利用，而选择面积较大的沼泽斑块作为夜栖地。主成分分析将其单独列入第二主成分(表 4)，说明沼泽面积独立地影响黑颈鹤对夜栖地的利用。

黑颈鹤利用浅水沼泽作为夜栖地也可能与保存能量有关。纳帕海全年平均温度低，温差较大，最冷月均温接近−4℃(Mu, 2007)。生活在高原高寒的环境中，如何保存能量是黑颈鹤必须面对的问题。由于水的比热容很大，水结冰后又有隔离作用，因而淡水湖的水温不会在 0℃以下(Sun, 2001)；冬季时，小湖泊水温高于周围空气温度，并向周围输出热量(Chen & Yu, 1983)；而白天时，湖泊水体吸收较多太阳辐射，水温低于地温，在夜间水温则高于地温(Yu & Lu, 1996)。因此推测：黑颈鹤为了保存能量，选择了温度可能较高又适合站立的浅水水域作为夜栖地。

3.5　保护建议

为了给黑颈鹤提供一个良好的夜栖环境，根据以上讨论，针对其夜栖时对浅水环境的依赖性，再考虑到纳帕海冬季较大的水位变化，提出以下几点水位管理建议：(1) 纳帕海在 10—11 月水位最高，浅水沼泽较少，开闸放水可为黑颈鹤提供较多的夜栖环境，但考虑到雁鸭类需要较大水体，所以建议此时适当开闸放水以增加浅水环境；(2) 12 月至翌年 3 月是纳帕海水位下降最快的时期，此时应适当关闸蓄水，以降低浅水沼泽消失的速度；(3) 4—5 月为越冬后期，大部分雁鸭类已经迁离，越冬黑颈鹤的数量因不断迁徙而减少，考虑到黑颈鹤需要补充部分动物性食物以利于迁徙，故应开闸放水，使鱼类食物更加集中而利于其捕食；再者，纳帕海为季节性湖泊，水退去后可能有利于湖底某些植物生长，从而在冬季为迁徙回来的黑颈鹤和其他水鸟提供更多的隐蔽条件和食物资源。

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人为干扰下宁夏贺兰山岩羊反应的群体差异

BACK

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摘要：野生动物对人类的非资源利用性的干扰具有不同的反应，这些反应的差异依赖于物种自身和外界生境中不同的因子。2009 年 7—8 月和 2009 年 12 月—2010 年 1 月在宁夏回族自治区贺兰山苏峪口国家森林公园，选定 95.87 km^2 的调查区域内设四条样线，总长度为 18.3 km，通过观察岩羊的瞬时反应距离，比较了不同干扰源、群体大小和群类型下，岩羊无反应行为、警戒反应行为和逃跑反应行为距离的差异。结果表明：(1) 相对于车辆，岩羊对行人的干扰更加敏感(U=8.69, P<0.001)；(2) 当群体大小分为$\leqslant$3 的小群和$>$3 大群时，小群岩羊的警戒反应行为距离显著大于大群(Z=2.165, P=0.03)，当群体大小分为$\leqslant$5 的小群和$>$5 的大群时，小群岩羊的逃跑反应行为距离显著大于大群(Z=2.003, P=0.045)；(3) 雌幼群、雄性群和混合群这 3 种不同的群类型之间的无反应行为距离无显著差异，雄性群的警戒行为距离显著大于雌性群和混合群的警戒行为距离(Z=2.746, P=0.006; Z=3.589, P<0.001)，雌性群的逃跑反应行为距离显著大于混合群的逃跑反应距离(Z=2.376, P=0.017)；(4) 混合群内的雌性和雄性的 3 种反应行为无显著差异。

关键词：岩羊；人为干扰；干扰源；瞬时反应距离；群体差异
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Group differences in responses of *Pseudois naynaur* to human disturbance in Helan Mountain, Ningxia Hui Autonomous Region

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Abstract: Wild animals respond differently to nonconsumptive human activity and such variation depends on multiple factors. We explored the behaviors of *Pseudois naynaur* and recorded the distance of their responses in Suyu Kou National Forest Park, Helan Mountain, Ningxia Hui Autonomous Region. We categorized their behavioural responses as no response, vigilance and flight and recorded the response initiation distance. We compared distances according to disturbance source, group size, group type and sex. Our results showed that *Pseudois naynaur* showed stronger responses to humans than vehicles. The distance at which the subject of the group was vigilant in small group (group size less than three) was significantly more than that of larger groups (group size more than three). The flight initiation distance in small groups (less than five) was significantly more than bigger groups. The distance of no response behavior did not vary between all male, female or mixed groups. The distance of vigilance behavior when the subject of the group first encountered the disturbance in male groups was significantly greater for female and mix groups, flight initiation distance in female groups was greater than that of mixed groups. In the mixed group, no significant variation on sex was found among all three types of behaviors.

Key words: Blue sheep (*Pseudois naynaur*); Human disturbance; Disturbance source; Response initiation distance; Sexual variation; Group differences

人类活动对自然生境(wilderness)的非消耗性利用(non-consumptive)是一种非资源获取性(non-extractive)利用(以下简称人为干扰)(David, 2003)。它包括生态旅游、交通等。这种人为干扰对

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自然环境造成的威胁正在急剧上升(Flather & Cordell, 1995)。这些负面影响包括野生动物行为改变, 例如突然停止取食、很快逃跑、繁殖行为的改变(Knight & Cole, 1995)、干扰野生动物的自然生态过程、改变物种的种间关系(Geist, 1978)、造成野生动物栖息地利用方式异常(Hamr, 1988; Gander & Ingold, 1997)以及生境生态承载力下降等(Light & Weaver, 1973)。这些对生态系统的潜在危害是不可忽视的。

在研究人为干扰对动物逃跑行为的影响时, 逃跑瞬时距离(flight initiation distance)是普遍使用的方法(Miller et al, 2006; Taylor & Knight, 2003; Recarte et al, 1998)。因此, 动物对不同干扰反应的警戒距离、逃跑瞬时距离可以用来确定和调整人类对该物种的最小接近距离(Rodgers & Smith, 1995)。Burger & Gochfield (1991)认为, 逃跑瞬时反应距离越大, 该物种对人类干扰的耐受性越小。这样就可以在当地和更大的区域水平指导野生动物的保护(Gill & Sutherland, 2000)。Knight & Cole(1995)认为当动物采取反捕食行动时会依赖于它们所在的群体大小、年龄和性别, 但是这些因素的影响并不一致(Stankowich, 2008), 把这些因素和动物生存的环境因素综合考虑, 可以较深入理解物种对人为干扰的反应机制。

从 1991 年起, 宁夏贺兰山国家级自然保护区开展旅游活动。岩羊(*Pseudois nayaur*) 是贺兰山最常见的野生偶蹄类, 并成为当地主要的观赏物种之一。因此, 在野生动物和人类交互作用较强的旅游地, 研究动物对人类干扰的反应以及不同环境因子下, 动物所反应的差异可以有效地用来指导管理者规划旅游区(Knight & Gutzwiller, 1995)。对此, 我们于 2009 年 7—8 月和 2009 年 12—2010 年 1 月, 在宁夏贺兰山国家级自然保护区的苏峪口国家森林公园对野生岩羊的人为干扰反应进行了研究, 其研究内容: (1)群体大小是影响动物对干扰的反应因素之一, 那么岩羊是否也存在这种类似的群体“稀释效应”; (2)雌雄动物由于生理和生活周期的差异, 对干扰的反应不同, 那么贺兰山岩羊的雌雄个体对干扰的反应是否存在差异。

1 材料与方法

1.1 研究区域概况

研究地区位于宁夏贺兰山国家级保护区苏峪口(38°42′N～38°46 ′N , 103°42 ′E～106° E) , 公园总面积为 95.87 km^2, 平均海拔 1 000～2 800 m。宁夏百科全书编撰委员会(1998)里把宁夏季节的时间划分为: 春季(4 月 11 日—6 月 20 日), 夏季(6 月 21 日—8 月 10 日), 秋季(8 月 11 日—10 月 10 日), 冬季(10 月 11 日—4 月 10 日)。作为贺兰山自然保护区内的国家级森林公园, 苏峪口是银川主要的旅游景点之一, 四季都有游客前往。Liu et al(2007)估计苏峪口有岩羊数量为 23 群 175 只。

1.2 研究方法

1.2.1 样线设置 2009 年 7 月—8 月, 6:30—10:30 和 15:00—19:30, 以及 2009 年 12 月—2010 年 1 月 8:00—12:00 和 14：00—17：30, 我们在研究地区根据苏峪口历次调查发现岩羊分布较集中的地区, 选择设置了森林公园主干道(9.8 km)、灵响路(3.5 km)、樱桃沟(3 km)汪沟(2 km)四条样线, 样线宽度为 6 m, 总长度为 18.3 km。

1.2.2 岩羊人为干扰反应行为观察 我们根据研究地区岩羊群的构成, 将岩羊群体分为 3 类: (1) 雌性群, 指观察个体为雌性, 所在群体中只包括雌性个体或者包括雌性个体和幼体, 无法分辨雌雄的亚成体划为此类; (2) 雄性群, 指观察个体所在群体只有雄性个体, 单个的雄性个体也包括在此类; (3) 混合群, 指观察个体所在群体既有雌性, 又有雄性, 具体观察时则进一步区分混合群雌性个体和雄性个体(Schaller, 1977)。

研究地区人类活动对岩羊的干扰主要来自公路上的行人和车辆。夏天, 森林公园开放, 常有旅游车辆经过, 车速一般为 40 km/h 左右。在评估车辆干扰时, 记录车辆经过时的岩羊群体中第一个个体注意到车辆时的反应行为类型(Taylor & Knight, 2003)。冬天, 旅游区关闭, 几乎没有车辆, 只评估行人干扰下岩羊的群体差异。在评估行人干扰时, 两名观察者身着暗色服装(Gutzwiller et al, 1997), 以大约 50 m/min 的行走速度, 记录公路两边岩羊的反应。当看见岩羊群体的时候, 一人使用 Yardage pro 800 激光测距仪记录群体内第一个反应的个体的行为和瞬时反应时离观察者的距离; 另一人在岩羊群体发生反应之后快速用望远镜分辨群体内雌性成年个体、雄性成年个体、亚成体、幼体(Wang et al, 1998)的数量。

我们把观察到岩羊的反应行为分成 3 类: 第一类, 无反应行为, 岩羊没有注意到干扰源或岩羊虽

然注意到干扰源，但是继续持续原来的行为；第二类，警戒行为，岩羊抬头注视干扰源，但是不走开；第三类，逃跑行为，岩羊注意到干扰源之后迅速离开(Treves, 2000)。

1.3 数据处理

1.3.1 岩羊对不同干扰源的反应差异 采用两个样本频次数据的假设测验(Sokal & Rohlf, 1995)来比较岩羊对车辆和行人这两种干扰源的反应行为差异。

1.3.2 群体大小对岩羊反应距离影响 以三类反应行为为区组研究群体大小对岩羊群不同反应行为类型反应距离的影响。使用统计软件 SPSS11.0 (SPSS, 2002)中的 Shapiro-Wilk 方法进行正态分布检验，发现不同群体大小的三种反应(无反应行为、警戒反应以及逃跑反应)距离是不符合正态分布的(Shapiro-Wilk tests of normality $P < 0.05$)。所以，用 Mann-Whitney *U* 测验比较不同群体大小对岩羊反应距离差异。

群体大小的确定是通过不同的组合使用 Mann-Whitney *U* 测验而划分的。当群体大小在≤3 头和>3 头时，其警戒行为出现显著差异。因此，在定义该反应行为的群体大小时，以群内个体≤3 头为小群，群内个体>3 头为大群；当群体大小在≤5 头和>5 头时，逃跑行为出现显著差异。因此，在定义该反应行为的群大小时，以群内个体≤5 头为小群，群内个体>5 头为大群。在检验无反应行为差异时，不同的群体大小下显著差异。

1.3.3 群体类型对岩羊反应距离的影响 在比较不同群体类型(雌性群、雄性群、混合群)之间反应距离的差异时，由于 3 种行为反应距离不符合正态分布，用 Mann-Whitney *U* 测验进行两两检验。

在比较混合群内部雌性和雄性反应距离差异时，根据 Shapiro-Wilk 正态分布检验，无反应行为距离和警戒反应距离是符合正态分布的，由独立样本 *t* 检验过程里 Levene's Test for Equality of Variances 判断两种行为下雌雄反应距离的方差齐性(对于无反应行为，$F_{(1,\ 181)} = 0.445$, $P = 0.506$；对于警戒反应行为，$F_{(1,\ 116)} = 0.056$, $P = 0.813$)，方差齐，用 *t* 测验。而逃跑反应距离在雌性和雄性中均不符合正态分布，用 Mann-Whitney *U* 测验。

2 结 果

2.1 不同干扰源下岩羊反应差异

当以人作为干扰源的时候，我们观察到了 429 只次，其中无反应为 78 只次，占总样本量的 18.2%，将警戒反应和逃跑反应归为有反应行为，为 351 只次，占总样本量的 81.8%。当以车辆作为干扰源的时候，我们收集了 103 只次，其中无反应行为为 62 只次，占总样本量的 60%，有反应行为的样本是 41 只次，占总样本量的 40.0%(表 1)。采用两样本频次数据 *t* 检验发现岩羊对不同的干扰源的反应有显著差异($U = 8.69$, $P < 0.001$)。岩羊对人的反应显著强于对车辆的反应，因此将行人作为干扰源作进一步分析。

表 1 两种干扰源下宁夏贺兰山岩羊反应行为比较

Tab. 1 Comparisons between two disturbing sources in responses of *Pseudois naynaur* in Helan Mountain, Ningxia Hui Autonomous Region

干扰源类型 Type of disturbance source	样本总数 The total number of sample	无反应行为比例 (%) Percent of no responses	有反应行为比例(%) Percent of having responses			*t* 检验 *t* test
			总计 Total	警戒 Vigilance	逃跑 Flight	
人 People	429	18.2	81.8	18.9	62.9	U=8.69 P<0.001
车 Vehicle	103	60.0	40.0	12.6	27.4	

2.2 群大小对岩羊反应距离影响

对于警戒反应行为，小群(群内个体数 ≤ 3 头，$n = 124$)出现警戒反应行为的距离显著地大于大群(群内个体数 > 3 头，$n = 57$)($Z = 2.165$, $P = 0.036$)。对逃跑反应行为，当群内个体数分为≤5 头和>5 头时，小群的逃跑行为反应的距离显著大于大群的逃跑反应距离($Z = 2.003$, $P = 0.045$)。而无反应行为在不同的群大小之间没有显著差异(表 2)。

2.3 群类型对岩羊反应距离的影响

在雌幼群、雄性群、混合群 3 种类群中，观察到无反应行为个体次数分别是 18、21 和 183 只次；观察到警戒行为个体次数分别是 30、33 和 118 只次；观察到逃跑行为个体次数分别是 58、29 和 149 只次。

同一种行为下，对三种群类型的反应距离用 Mann-Whitney *U* 进行两两样本检验后发现，群类型差异对无反应行为无显著差异(Z=0.775, P=0.443;

表 2 宁夏贺兰山岩羊群体大小对干扰反应行为的差异

Tab. 2 The difference of responses of *Pseudois naynaur* in different group size in Helan Mountain, Ningxia Hui Autonomous Region

群大小 group size	无反应 No responses		警戒 Vigilance*		逃跑 Flight**	
	平均值±*SD* Mean±*SD*(m)	Mann-Whitney *U* test *Z*, *P*	平均值±*SD* Mean±*SD*(m)	Mann-Whitney *U* test *Z*, *P*	平均值±*SD* Mean±*SD*(m)	Mann-Whitney *U* test *Z*, *P*
小群 Small group	145.40±57.92 (22～399, *n*=156)	*Z*=1.120, *P*=0.263	145.62±72.20 (15～37, *n*=124)	*Z*=2.165, *P*=0.030*	110.82±57.81 (6～288, n=169)	*Z*=2.003, *P*=0.04**
大群 Big group	139.26±54.82 (29～280, *n*=66)		126.23±60.92 (10～280, *n*=57)		95.32±56.61 (5～254, *n*=67)	

*小群：群体内个体数≤3 头；大群：群体内个体数>3 头。*group size that is less than 3 is defined as small group, group size that is more than 3 is defined as big group.

小群：群体内个体数≤5；大群指群体内个体数 >5 头。group size that is less than 5 is defined as small group, group size that is more than 5 is defined as big group.

表 3 宁夏贺兰山岩羊在群类型间对干扰反应行为的差异*

Tab. 3 The different responses in different group types of *Pseudois naynaur* in Helan Mountain, Ningxia Hui Autonomous Region*

群类型 Group type	无反应 No response	警戒 Vigilance	逃跑 Flight
	平均值±*SD* Mean±*SD*(m)	平均值±*SD* Mean±*SD*(m)	平均值±*SD* Mean±*SD*(m)
雌幼群 Female group	144.83±57.39 (30～219, *n*=18)	130.60±71.39^{ac} (37～337, n=30)	117.10±59.93^{a} (30～288, *n*=58)
雄性群 Male group	166.44±74.41 (22～399, *n*=21)	189.83±81.33^{b} (50～374, *n*=33)	104.66±65.03^{ab} (15～219, *n*=29)
混合群 Mix group	147.94±81.86 (29～280, *n*=183)	128.77±65.79^{c} (25～-300, *n*=118)	110.48±54.13^{b} (25～211, *n*=149)

*用 Mann-Whitney *U* 检验差异性，在无反应组无显著差异(*Z*=0.775, *P*=0.443; *Z*=0.427, *P*=0.669; *Z*=0.716, *P*=0.474)；在警戒组中，雄性群的反应距离显著大于雌性群的反应距离(*Z*=2.746, *P*=0.006)，也显著大于混合群的反应距离(*Z*=3.589, *P*<0.001)；在逃跑反应中，雌性群的反应距离显著大于混合群的反应距离(*Z*=2.376, *P*=0.017)。

^{abc} 分别表示不同的类群之间的差异程度。当不同群类型的行为进行两两比较时，拥有不同字母角标的组之间差异显著。

*Mann-Whitney *U* Test is used to analyze the difference in distance from observers when having and not having responses between female group, male group and mix group. In the case of no responses, there is no significant differences (*Z*=0.775, *P*=0.443; *Z*=0.427, *P*=0.669; *Z*=0.716, *P*=0.474). In the case of vigilance behavior, the distance of male group from the observers is significantly greater than female group(*Z*=2.746, *P*=0.006) and mix group(*Z*=3.589, *P*<0.001). The distance when female group fled significantly greater than mix group(*Z*=2.376, *P*=0.017).

abc stands for the extent of distance of responses between three group types. The blocks with different superscript letters have significant differences.

Z=0.427, *P*=0.669; *Z*=0.716, *P*=0.474)。在警戒行为中，雄性群的反应距离显著大于雌性群的反应距离(*Z*=2.746, *P*=0.006)，也显著大于混合群的反应距离(*Z*=3.589, *P*<0.001)，而其他群类型间无显著差异。在逃跑反应中，雌性群的反应距离显著大于混合群的反应距离(*Z*=2.376, *P*=0.017)，而其它群类型间无显著差异(表 3)。

当个体来自于混合群时，根据个体的性别分为雌性和雄性，比较雌性和雄性的 3 种反应行为下的距离差异。无反应行为下的雌雄反应距离无显著差异(*t* = 0.014 , *P* = 0.671)；警戒行为下雌雄反应距离无显著差异(*t* = 0.014, *P* = 0.989)；逃跑反应行为距离在雌雄之间无显著差异(*Z* = 0.078, *P* = 0.938)(表 4)。

表 4 宁夏贺兰山岩羊在混合群内对干扰反应行为的差异

Tab. 4 The different responses in different group types of *Pseudois naynaur* in Helan Mountain, Ningxia Autonomous Region

混合群 Mix group	无反应 No responses		警戒 Vigilance		逃跑 Flight	
	平均值±*SD* Mean±*SD*(m)	*t* 检验 *t*-test	平均值±*SD* Mean±*SD*(m)	*t* 检验 *t*-test	平均值±*SD* Mean±*SD*(m)	Mann-Whitney *U* test Z, *P*
雌性 Female	153.62±56.88 (29～287, *n*=91)	*t*=0.426 *P*=0.671	129.28±63.95 (25～300, *n*=36)	*t*=0.014 *P*=0.989	101.33±56.78 (5～254, *n*=83)	*Z*=0.078 *P*=0.938
雄性 Male	157.41±63.57 (22～399, *n*=92)		123.50±65.06 (10～280, *n*=82)		99.99±56.84 (6～254, *n*=66)	

3 讨　论

3.1 干扰源对岩羊的干扰反应行为的差异

MacArthur et al(1982)认为干扰源的不可预测性是动物衡量危险程度的重要因素。可预测性较高的干扰比较规律, 这样容易使动物产生对干扰源的适应行为(Cederna & Lovari, 1985; Tyler, 1991; Cassirer et al, 1992; Lamerenx et al, 1992), 表现在动物对这类干扰的行为反应强度降低(Knight & Cole 1991; Borkowski et al, 2006)。行人对苏峪口岩羊的干扰强度显著强于车辆(表 1), 正是因为车辆往往有固定的行进路线(景区的公路车道), 属于重复性、可预测性较强的干扰源(Knight & Gutzwiller, 1995); 而游人常常会随意步行, 属于不可预测性较高的干扰源。因此, 相比游人, 岩羊对车辆警戒强度较低。此外, 岩羊一直是贺兰山主要的偷猎对象(宁夏贺兰山国家级自然保护区内部资料, 2006), 而偷猎者往往是徒步者, 因而强化了岩羊对普通行人的行为反应。Papouchis et al(2001)对沙漠大角羊(*Oviscanadensis nelsoni*)的研究也获得了相似的结果。因此, 岩羊对不同干扰源的显著差异是其对不同类型人为活动干扰的一种行为适应机制。

3.2 群大小对干扰反应行为的作用

警戒行为是动物很重要的反捕食策略(Bednekoff & Lima, 1998)。动物在评估捕食风险时, 警戒行为是其评估过程中的主要行为, 而逃跑行为是确定了较高的被捕食机率后的反应行为。本研究显示这两种行为, 小群岩羊中的反应行为距离均显著大于大群岩羊反应行为距离(表 2)。这些现象说明, 岩羊群存在“稀释效应”(dilution effect), 即在较大的群内, 个体平均被捕食机率降低(Lima & Dill, 1990)。因此, 个体的警戒强度会降低。同时, 大群体中有专司警戒的个体(Stankowich, 2008), 这样大群内的个体感觉更为安全。因此, 通常观察者可以更为接近大群, 而小群在较远距离就开始警戒或者逃跑。这种是在大型集群食草动物中典型的行为策略, 在 Fallow deer (*Dama dama*) (Recarte et al, 1998)、Rocky mountain elk(*Cervus elaphus*)(Childress & Lung, 2003)和 Springbok (*Antidorcas marsupialis*)(Burger et al, 2000)中均有类似现象的报道。

3.3 群类型间干扰反应行为的差异

集群类型对岩羊反应的影响表现在警戒行为和逃跑行为中。在警戒反应中, 雄性群的警戒反应距离最大, 其次是雌性群(表 3)。雄性群警戒性更强的现象在其它大型食草动物中已有报道(Burger et al, 2000; Prins & Iason, 1989; Steenbeek et al. 1999)。相关的研究表明, 雄性个体会更多地抬头寻找交配的机会, 或者对竞争者保持警惕(Burger et al, 2000; Burger & Gochfeld, 1994)。另一方面, 雄性个体通常是人类猎杀的对象(Stankowich & Coss, 2005), 因而使得雄性个体对于人类活动的警惕性更高。偷猎岩羊情况在贺兰山经常发生, 雄性成年岩羊因其较大的角而成为主要的猎杀对象(宁夏贺兰山国家级自然保护区内部资料, 2006)。这些都会使雄性个体更为警觉, 警戒距离较雌性个体更远。

在逃跑行为中, 雌幼群对行人的靠近也非常敏感, 显著大于混合群的逃跑反应距离(表 3)。在我们的样本中, 携带有幼体的雌幼群, 占 83%。雌性个体为了使它的繁殖成功率达到最大, 倾向于保护它的幼体免受伤害(Main et al, 1996; Ciuti et al, 2008)。因此, 雌性个体会选择带领幼仔快速逃离过分靠近的人类带来的潜在威胁。

由于岩羊对可预测性较低的人为干扰更为警觉, 对其正常活动的影响也更大。因此, 我们建议公园管理者应进一步规范游客旅游娱乐活动区域, 尽量减少对岩羊适宜生境的干扰。同时, 组织游客观光旅游时, 应考虑减少在岩羊生命周期中重要时期, 如交配繁殖期时, 对岩羊的干扰。另外, 随着保护区旅游景点的开发强度增大, 对岩羊的干扰将会更加强烈。因此, 对岩羊人为干扰的适应机制值得进一步深入研究。

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普通长翼蝠食性结构及其回声定位与体型特征

BACK

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摘要：在普通长翼蝠（*Miniopterus fuliginosus*）的捕食区内用灯诱法和网捕法调查潜在食物（昆虫）种类；用粪便分析法鉴定普通长翼蝠的食物组成，发现其主要捕食体型较大的鳞翅目和鞘翅目昆虫，体积百分比分别为 55%和 38%。普通长翼蝠具有相对狭长的翼，翼展比为 6.94 ± 0.13；翼载为（9.85 ± 0.83）N/m^2，相对较大。飞行状态下普通长翼蝠的回声定位叫声为调频下扫型，声脉冲时程为（1.45 ± 0.06）ms，脉冲间隔为（63.08 ± 21.55）ms，主频较低，为（44.50 ± 2.26）kHz。研究表明，普通长翼蝠的形态特征和回声定位特征与其捕食行为有着密切的联系。

关键词：粪便分析；食物种类；形态；普通长翼蝠
中图分类号：Q959.833; Q811.213; Q958.122.5　　**文献标志码：**A　　**文章编号：**0254-5853-(2011)02-0163-05

Dietary composition, echolocation pulses and morphological measurements of the long-fingered bat *Miniopterus fuliginosus* (Chiroptera: Vespertilioninae)

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Abstract: We investigated food (insect) availability in foraging areas utilized by the long-fingered bat *Miniopterus fuliginosus* using light traps, fish netting and fecal analysis. The dominant preys of *M. fuliginosus* were Lepidoptera (55%, by volume percent) and Coleoptera (38%) of a relatively large body size. *M. fuliginosus* has relatively long, narrow wings and a wing span of 6.58 ± 0.12 and high wing loading of 9.85 ± 0.83 N/m^2. The echolocation calls of free flying *M. fuliginosus* were FM signals, with a pulse duration of 1.45 ± 0.06 ms, interpulse interval of 63.08 ± 21.55 ms, and low dominant frequency of 44.50 ± 2.26 kHz. This study shows that the morphological characteristics and echolocation calls of long-fingered bats are closely linked to their predatory behavior.

Key words: Fecal analysis; Diet composition; Morphology; *Miniopterus fuliginosus*

普通长翼蝠（*Miniopterus fuliginosus*）又称为折翅蝠、大长翼蝠，广泛分布于亚洲、南欧、北非、所罗门群岛及澳大利亚的北部和东部（Simmons, 2005; Tan, 1992），国内见于华北、西南和华南地区，通常集群生活于温暖潮湿的洞穴中（Luo et al, 1993）。食虫蝙蝠主要捕食鞘翅目、鳞翅目和双翅目昆虫（Kunz & Fenton, 2003）。昆虫几丁质的体壁或前翅，还有膜质翅等常常不易被消化而随粪便排出，因而粪便分析可以较好地用来研究其食物组成（Belwood & Fenton, 1976; Black, 1974; Kunz &

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Whitaker, 1983; Whitaker, 1988）。Belwood （1979）认为，在蝙蝠粪便中食物成分的多样性很高，因而可以通过粪便分析检测出其捕食昆虫的种类。Kunz & Whitaker（1983）也发现用粪便分析法可以比较精确地测出蝙蝠的食性。另外，蝙蝠的食性还因季节（Bauerová & Červený, 1986; Catto et al, 1994; Jones, 1990; Waters et al, 1999）、种类（Warner, 1985）、地理（Johnston & Fenton, 2001; Zhang et al, 2004）、性别（Belwood & Fenton, 1976; Kunz, 1974）和年龄（Rolseth et al, 1994）不同而存在差异。对于其食性，Luo et al （1993）认为普通长翼蝠喜欢捕食静止的昆虫如松毛虫（Lasiocampidae, Lepidoptera）、金龟子（Scarabeidae, Coleoptera）等；而 Funakoshi & Takeda （1998）通过粪便分析后发现其主要捕食体长在 5～25 mm 的鳞翅目、双翅目、毛翅目和鞘翅目昆虫，但其仅研究了 7 月份的食性。Kuramoto （1972）对普通长翼蝠的体型进行过研究，但没有报道其翼型，如翼展比和翼载这些重要的生态形态结构参数。Liu et al（2004）对普通长翼蝠福建亚种不同行为状态下的回声定位声波做了研究。研究显示，蝙蝠的翼型、捕食行为和飞行速度间存在联系（Altringham et al, 1998）。本文试图通过粪便分析普通长翼蝠的食物组成，以及对其体型和回声定位信号特征的研究，来探讨其形态和回声定位特征与其捕食行为的关系。

1 材料与方法

野外工作在贵州省安顺市蔡官驿马寨村及大坡洞村进行。该地海拔 1380～1490 m，地形以低山丘陵为主，岩溶发育，属于中亚热带气候，年均温 14～16 °C，降雨量 1200～1300 mm，气候温和湿润。在大坡洞村偏东北方向的小山顶部，有一称为塘官大坡洞的山洞（26° 22' 42.0"N, 106° 04' 16.0"E），洞口朝向西南，高约 2 m，宽约 10 m。洞内高度 5～10 m，宽约 5 m，洞长约 4000 m。距大洞口约 80 m 处为一小洞口（80 cm × 50 cm）。蝙蝠的栖息地在该小洞内。洞内湿度为 74%～88%，温度为 18～24 °C。有一地下暗河流经洞内。野外工作分别于 2005 年 7 月底至 8 月初和 9 月底至 10 月初进行，共调查 2 次，每次各自连续调查 10 d。

从夜间 21：00 至次日 4：00 在小洞口处悬挂雾网，每隔 0.5 h 进洞查看一次，捕捉到的蝙蝠记录种类、性别，测量部分个体体重（精确到 0.1 g）、体型参数（精确度为 0.1 mm），参照 Norberg & Rayner （1987）的方法测量翼面积（wing area, 展开翼膜后的身体面积、翼膜面积和尾膜面积之和，不包括头部）、翼展（wing span, 展开翼膜后两侧翼尖之间的距离），计算翼载（wing loading, 体重/翼面积）、翼展比（aspect ratio, 翼展的平方/翼面积）。将捕获的回洞成年蝙蝠置于干净小布袋内，每袋一只，编号并记录性别。次日清晨收集粪便并将蝙蝠释放。粪便干燥后，将每只个体的粪便分别置于小玻璃瓶内密封保存，待鉴定。在释放蝙蝠的同时我们用超声波探测器（D980, Pettersson Elecktronik）记录其自由飞行状态下的回声定位信号，经频率转换为原始频率的 1/10 后录入电脑，用 BatSound 软件（Pettersson Elektronik AB）进行分析（哈明窗 FFT points 1024，频率分辨率为 280 Hz，时间分辨率为 4.6 ms）。分析的声波参数主要包括：脉冲时间（pulse duration）、脉冲间隔（pulse interval）、峰频（Peak frequency, PF），并计算出能率环（脉冲时间占脉冲时间与脉冲间隔之和的百分比）。

蝙蝠在黄昏时外出觅食，因当地生境相对简单，洞周围山上为石灰岩藤刺灌丛及玉米庄稼地，以及村子周围有小片的常绿阔叶林、半常绿林呈斑块状分布。在灌丛和庄稼地上空支架雾网，捕捉蝙蝠（在记录捕捉到蝙蝠的性别后，随即释放）。因在林中架网有困难，便在村周围小片林地之间的空地上支架雾网。这样，如果蝙蝠在林地中捕食，便能够在此捕捉到来往于林地间的蝙蝠。雾网宽约 2 m，长约 6 m，距地面约 2～3 m。根据 20 个晚上的网捕结果，我们仅在灌丛及玉米庄稼地上空捕捉到蝙蝠，而林地之间的空地上空并没有捕捉到普通长翼蝠，从而确认普通长翼蝠主要在灌丛和庄稼地上空（主要为玉米庄稼地）捕食。与网捕蝙蝠同步，每天于捕食时间内在蝙蝠的捕食生境用灯光诱捕昆虫，同时利用昆虫网来网捕昆虫，作为蝙蝠食物可利用度的样本，共计 20 个晚上。把昆虫样品保存在 70%的酒精中，作为粪便残余物鉴定的参照标本（Whitaker, 1988）。参考郭振中编著的《贵州农林昆虫志》（Guo et al, 1987）鉴定捕捉到的昆虫样本，并测量其体长。

把粪便先在 70%的异丙醇中至少浸泡 12 h （Belwood & Fenton, 1976），然后将粪便颗粒置于培养皿中，并在培养皿底部置一细筛，参考 Kunz & Whitaker（1983）、Kunz & Nagy（1988）的方法，在

解剖镜下将粪便中的昆虫残骸鉴定到目，分类依据参照标本（Whitaker, 1988）。同时利用网格计数法来计算各目昆虫的体积百分比（该目昆虫的体积占总样品体积的百分比），分析其食物组成。所有数据使用 SPSS 13.0 进行分析，分析的数据均以平均值±标准差（Mean ± *SD*）表示。

2　结果与分析

2.1　体型特征

普通长翼蝠体型中等，前臂长为（47.69 ± 1.11）mm(n = 53)，体重（13.6 ±1.1）g(n = 53)，翼载较大，为(9.85 ± 0.83) N/m^2（n = 53）。翼相对较狭长，翼展比为[(6.94 ± 0.13)(n = 53)]，结果如表 1 所示。

表 1　普通长翼蝠的体型参数（n = 53）

Tab. 1　Morphological measurements of *Miniopterus fuliginosus*（n = 53）

形态测量 Morphological measurement（mm）	平均值 ± 标准差 Mean ± *SD*	参数 Parameter	平均值 ± 标准差 Mean ± *SD*
前臂长 Forearm length	47.7 ± 1.1	体重 Body mass（g）	13.6 ± 1.1
头体长 Body length	57.5 ± 1.0	翼展 Wing band（cm）	30.9 ± 0.6
尾长 Tail length	56.1 ± 1.3	翼面积 Wing area（cm^2）	138.0 ± 4.0
胫长 Shank length	21.5 ± 0.3	翼载 Wing loading（N/m^2）	9.85 ± 0.83
耳长 Ear length	8.7 ± 1.3	翼展比 Aspect ratio	6.94 ± 0.13
后足长 Feet length	10.8 ± 0.5		

2.2 回声定位信号分析

飞行状态下普通长翼蝠回声定位声波的声谱为下扫调频（downward frequency-Modulated, DFM）型（图 1），其主频（peak frequency）为（44.50 ± 2.26）kHz，最高频率（max frequency）为（76.04 ± 2.82）kHz，最低频率（min frequency）为（36.99 ± 0.57）kHz，脉冲时程（duration）为（1.45 ± 0.06） ms，脉冲间隔（interpulse interval）为（63.08±21.55） ms，能率环（duty cycle）为 2.2%。

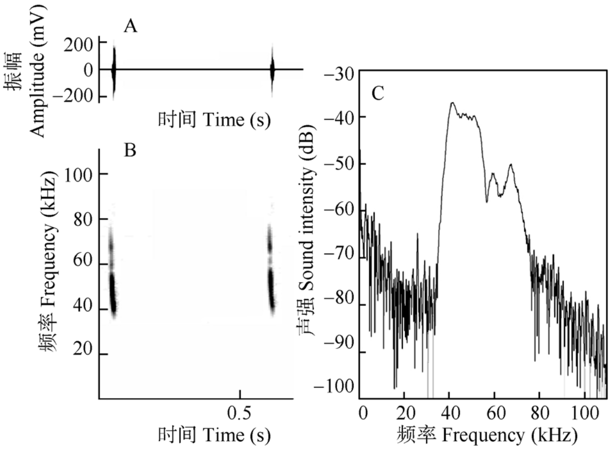

图 1　普通长翼蝠飞行状态下回声定位叫声

Fig. 1　The echolocation pulses of *Miniopterus fuliginosus* at flying status

A：波形图; B：声谱图; C：能谱图.

A: Oscillogram; B: Sonogram; C: Power spectrum.

2.3　食物组成

该地区普通长翼蝠的潜在食物量以鳞翅目（Lepidoptera）最多（34%），体积百分比超过总量的三分之一，其他依次为双翅目（Diptera）（24%）、鞘翅目（Coleoptera）（16%）和膜翅目（Hymenoptera）（4%）。每只个体至少随机分析粪便 5 粒，共计分析粪便 271 粒。食物中的昆虫残骸镜检并依据参照标本分类后发现，普通长翼蝠的食物组成主要有 4 个目的昆虫，分别为鳞翅目 55%（体长为 6～30 mm）、鞘翅目 38%（体长为 5～15 mm）、双翅目 2%（主要为体长 5 mm 左右的蚊类）以及膜翅目 1%（主要为体长不超过 5 mm 的小型蜂类）（表 2）。对比普通长翼蝠的食物组成与潜在食物量，用 Wilcoxon signed-ranks tests 检验分析发现，鞘翅目在其食物中的体积百分比显著多于其在潜在食物量中的体积百分比（$P < 0.01$），双翅目和膜翅目在其食物中的体积百分比则显著少于潜在食物量中的体积百分比($P < 0.01$)，而鳞翅目在食物中体积百分比与潜在食物量中体积百分比无显著差异($P > 0.05$)。

表 2　四类昆虫在捕食环境中和普通长翼蝠食物组成中的体积百分比（共 20 晚）

Tab. 2　Proportions of four insect groups in the bats foraging area and in the feces of *Miniopterus fuliginosus* for 20 nights

种 类 Orders	潜在实物量 Potential food（%）	食物组成 Diet composition（%）	*P*
鞘翅目 Coleoptera	16.0 ± 3.6	37.9±16.2	<0.01
鳞翅目 Lepidoptera	34.2 ± 10.6	54.9±16.3	>0.05
双翅目 Diptera	23.5 ± 5.3	2.2±1.8	<0.01
膜翅目 Hymenoptera	4.0 ± 1.8	1.0±0.8	<0.01

3 讨论

3.1 体型特征与捕食

翼载是蝙蝠生态形态结构最重要的参数之一，为体重与翼面之积的比值，描述的是蝙蝠单位翼面积上所承受的压力。这个参数与飞行速度呈正相关；而与飞行的灵活性呈负相关（Jennings et al, 2004）。翼载越大，说明其翼之面积相对越小，蝙蝠需要提高其飞行速度，从而使其较小的翼得到足够的上浮力，但同时以牺牲飞行的灵活性和机动性为代价。而飞行的灵活性不高，使得蝙蝠捕捉不到体型较小的猎物（Arita & Fenton, 1997）。翼展比也是蝙蝠生态形态结构最重要的参数之一，它描述的是翼的形状。具有高翼展比的蝙蝠具有狭长的翼，同时具有高效的飞行能力（Jennings et al, 2004），因为高翼展比可以使蝙蝠更有效地利用空气动力，从而在飞行中损失更少的能量（Norberg & Rayner, 1987）。Schnitzler & Kalko（1998）认为高翼展比的蝙蝠适合在植被上空快速的飞行捕食。普通长翼蝠具有较大的翼展比，说明其具有较狭长的翼，飞行速度快；同时，翼载也较大，导致飞行的灵活性较差。上述形态特征使其可能适合在相对空旷的环境中捕食。本研究的网捕结果也表明，普通长翼蝠的捕食区域主要是在相对开阔的庄稼地上方。

本研究通过分析普通长翼蝠的食物组成发现，其主要捕食体型较大的鞘翅目和鳞翅目昆虫，其中鞘翅目在其食物中的体积百分比显著多于其在潜在食物量中的体积百分比。而对环境中数量较多的体型较小的双翅目昆虫（主要是蚊子）则捕食较少，对环境中体型较小的膜翅目（大部分为体长不超过5 mm的小型蜂类）的捕食也较少，两者在其食物中的体积百分比均显著低于其潜在食物量中的体积百分比。对于飞行速度快而缺乏灵活性的普通长翼蝠而言，不可能像一些低翼载的蝙蝠那样采用“拖网式”的捕食方式大量猎取这类小型的昆虫，必须在保证高成功率的前提下捕食那些能够提供更高能量的较大昆虫以维持其较高的能量代谢。

3.2 回声定位信号与捕食

回声定位声波的频率和波长成反比，而蝙蝠探测目标时的最佳波长与目标长度相近，因此一般频率越高，猎物越小，频率越低，猎物越大（Wilkinson, 1995）。蝙蝠的回声定位声波在空气中传播时频率越高，其衰减的程度越强，从而使得蝙蝠探测的距离越短；相反，蝙蝠回声定位频率越低，其衰减的程度越弱，从而使得蝙蝠探测的距离也越远（Neuweiler, 1989）。频率的高低可以看出蝙蝠捕食环境的复杂性不同，一般地，在相对开阔的空间进行长距离飞行或捕食时，使用的回声定位叫声频率较低，而在复杂环境中进行飞行或捕食时使用的回声定位频率较高（Schnitzler & Flieger, 1983）。我们的研究发现，普通长翼蝠在飞行状态下的主频相对较低，其捕食环境为相对开阔的空间，同时倾向于捕食体型较大的猎物，这进一步验证了上述观点。

3.3 不同地理种群间的食性差异

同种蝙蝠的不同地理种群之间的食性存在差异（Johnston & Fenton, 2001; Zhang et al, 2004）。与日本鹿儿岛县普通长翼蝠食性研究结果（Funakoshi & Takeda，1998）相比，两地普通长翼蝠对双翅目的捕食存在较大差异，双翅目在 Funakoshi & Takeda（1998）的研究中，占普通长翼蝠食物组成的 23%，而在本研究中仅占 2%；在 Funakoshi & Takeda（1998）的研究中，普通长翼蝠捕食的为环境中体型较大的双翅目，如大蚊科（Tipulidae）昆虫（体长大约 10 mm）；而本研究普通长翼蝠的捕食环境中的双翅目大部分为体型较小的蚊子（体长大约 5 mm），蝙蝠对之捕食较少。此外，在 Funakoshi & Takeda（1998）的研究中，毛翅目（Trichoptera）和蜉蝣目（Ephemeroptera）昆虫也是普通长翼蝠食物的主要组成成分，而本研究没有发现普通长翼蝠对这两类昆虫的捕食。由于上述两类昆虫皆为水生昆虫（Zheng & Gui, 1999），本研究中普通长翼蝠的捕食环境主要为旱田，我们在此生境中没有捕捉到这两类昆虫；而在 Funakoshi & Takeda（1998）的研究中，这两类昆虫在捕食生境中大量存在，这说明捕食生境中潜在食物量的丰度不同也是导致不同地理种群间食性差异的原因。

综上所述，本研究从贵州普通长翼蝠的食物选择、体型及回声定位信号特征三方面进行分析和阐述，发现其形态特征和回声定位特征与其捕食行为有着密切的联系，为该物种的行为生态学及生活习性的进一步研究奠定基础。

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New records of bats from the northern region of the Peruvian Amazon

BACK

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Abstract: The northern Amazon Basin in Peru is one of the most diverse areas for small mammals in the world. In this work, I present information related to the diversity of bat species in the Amazonian region of Iquitos, Peru, where nearly 60% of the 152 bat species known to Peru recorded. Unlike in previous investigations in this area, bat surveys were designed to detect species living in urban and rural areas. The results have added a new bat species (*Eumops delticus*) to the Peruvian fauna, eight new species for the region around Iquitos (*Peropteryx macrotis*, *Peropteryx pallidoptera*, *Anoura caudifer*, *Lionycteris spurrelli*, *Vampyrum spectrum*, *Thyroptera lavali*, *Cynomops planirostris*, and *Molossus coibensis*), and a new species for Northeast Peru (*Eumops maurus*).

Key words: Chiroptera; Iquitos; Amazon; Checklist

秘鲁亚马孙北部地区蝙蝠新记录

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摘要：位于秘鲁的亚马孙盆地北部是世界小型哺乳动物多样性最高的地区之一。该文报道了亚马孙流域在秘鲁伊基托斯的蝙蝠物种多样性：这里的蝙蝠物种数约占秘鲁已知 152 个蝙蝠物种的 60%。与在该地区之前开展的研究不同, 本次调查范围为城市和农村地区。结果发现 1 个秘鲁新记录(*Eumops delticus*)、8 个伊基托斯新记录(*Peropteryx macrotis*、*Peropteryx pallidoptera*、*Anoura caudifer*、*Lionycteris spurrelli*、*Vampyrum spectrum*、*Thyroptera lavali*、*Cynomops planirostris* 和 *Molossus coibensis*)和 1 个秘鲁东北部新记录(*Eumops maurus*)。

关键词：翼手目; 伊基托斯; 亚马孙; 记录
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The Amazon Basin covers millions of square kilometers and is characterized by a gradient of increasing diversity from east to west (Emmons, 1984; Voss & Emmons, 1996). The great species richness of the Peruvian Amazon is mainly due to the high heterogeneity that results from a combination of environmental factors, edaphic and ecological conditions, and historical processes (Gentry, 1986; Salo et al, 1986; Kalliola et al, 1993; Tuomisto et al, 1995; Alvarez Alonso, 2002).

Iquitos is a region known worldwide for its high diversity of wildlife species (Gentry, 1988; Rodríguez & Duellman, 1994; Lamar, 1997; Díaz & Willig, 2004), including a high diversity of small mammals (Hice, 2003; Hice et al, 2004). Approximately 60% of the 152 species of bats in Peru can be found in this region around Iquitos (Pacheco, 2002). As a result of the intensive surveys conducted in this area, several new records of small mammal species have been added to the Iquitos region (Hice & Solari, 2002; Hice, 2003; Angulo & Díaz, 2004; Díaz & Willig, 2004; Hice et al, 2004). The studies of Hice et al (2004) carried out at the Reserva Nacional de Allpahuayo Mishana (25 km west of Iquitos) recorded 65 species of bats that made that area as the second richest area for bats species in Peru, after Parque Nacional de Manu. For other areas located in the Department of Loreto, 63 (Ascorra et al, 1993; Solari et al, 1999) and 57 species of bats (Fleck et al, 2002) were recorded.

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However, those surveys conducted in specific areas focused mainly on natural environments with variable degrees of human impact; they did not include suburban and urban areas. Thus, knowledge about bats of these urban environments was available only from specimens collected occasionally or found accidentally in towns (Avila-Flores & Fenton, 2005). Although the urbanization processes may have harmful effects on bats, leading to dramatic declines in diversity and abundance (Avila-Flores & Fenton, 2005; Oprea et al, 2009), it should be noted that they also provide shelter as well as food. Some species benefit from the concentrations of insects clustered around streetlights (Fenton, 1997; Everette et al, 2001). For these reasons, I decided to intensify collection efforts in urban and suburban areas, resulting in the inclusion of several species new to this area, as well as several new species for Peru.

1 Materials and Methods

The species reported here were collected from December 2002 to December 2006, at 14 collecting sites along the Iquitos-Nauta Highway (see Appendix I, Fig. 1), which passes through several districts of the Province of Maynas, Loreto Department. The overall study area is located in the "Iquitos region" (as referred to by Ortiz-S, 1997) and includes the northeastern Amazon Basin of Peru, and the adjacent part of southern Colombia. The region is dissected by several rivers and streams, and the elevation ranges from 100 to 220 m, with low-lying areas characterized by flooded forests (igapo) and higher areas supporting white sand forests (varillal) and upland forests (monte alto) (Ruokolainen & Tuomisto. 1993; Willig et al, 2007). The climate is relatively uniform, warm (average annual temperatures between 25 - 27°C), humid (annual mean humidity 85%), and rainy (annual mean precipitation 2700 mm) (Encarnación, 1985; Tafur Rengifo, 2001).

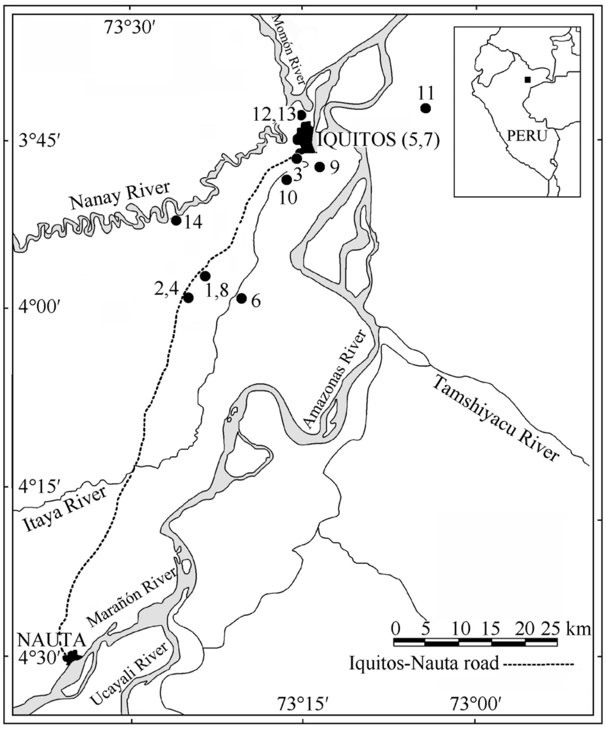

Fig. 1 Map of localities for collected bats (see details of localities in the Appendix I).

Map modified from Kalliola & Flores Paitán (1998).

The study sites included primary and secondary forests, as well as rural, suburban, and urban areas. All bats were captured with mist nets placed at different heights, from the ground up to the sub-canopy and canopy levels. Nets were set from 18:00 h until 01:00 h and were checked every hour. Some specimens were collected by searching diurnal roosts in tree cavities, foliage, culverts, and buildings, among other places.

Total capture effort was 60,552 net-meter-hours, and the capture effort by habitat was 13,806 net-meter-hours for primary forest, 16,890 for secondary forest, 12,648 for urban areas, 12,900 for rural areas, 1,812 for suburban areas, 720 for primary-secondary forest ecotones and 1,776 for secondary forest-rural area ecotones. A total of 5,510 specimens were captured, from which 3,436 were collected and 2,089 released. Of the total, 5,270 were captured in mist nets and 255 were captured in roosts.

External measurements, body mass, sex, and reproductive condition were recorded in the field for all specimens, following Díaz et al (1998). Voucher specimens were prepared as skins and skeletons or stored in alcohol. The specimens are still being catalogued. A portion of the specimens will be deposited at the Museo de Historia Natural, Universidad Nacional Mayor de San Marcos (UNMSM), Lima, Peru, and another portion will be deposited at the Colección Mamíferos Lillo (CML), Tucumán, Argentina. The acronyms used in the text are MMD (personal catalogue of María Mónica Díaz) and CML (Colección Mamíferos Lillo).

The external measurements were taken from fresh specimens using a ruler, and forearm and cranial measurements were taken with a digital caliper to the nearest 0.05 mm. All measurements were taken as described by Barquez et al (1999), but I add the condyle-incisive length, measured as the distance from the anteriormost plane of the upper incisors back to the posteriormost projection of the occipital condyles. The measurements and their abbreviations are as follows: total length (ToL), tail length (TL), hindfoot length (HFL), ear length (EL), forearm length (FA), weight (W), body mass in grams, greatest length of skull (GLS), condyle-incisive length (CIL), breadth of braincase (BB), least interorbital breadth (LIB), postorbital constriction (PC), zygomatic breadth (ZB), mastoidal breadth (MB), palatal length (PL), length of maxillary toothrow (LMxT), width across upper canines (C-C), width across upper molars (M-M), length of mandible (LM), and length of mandibular toothrow (LMdT).

The Specimens Examined indicates the amount of individuals collected per locality, their sex and their catalogue numbers. Additional Records are given for some species when they were registered in a nearby locality. Under Remarks, some general comments are added, mainly related to field, systematic, or distributional observations, as well as activity and habitat. The new records are explained in the species accounts.

2 Results

The intensive mist-netting and searching for bats in roosts, conducted over nearly five years, has allowed for the extension of the previously known distributions for ten species (families Emballonuridae, Phyllostomidae, and Molossidae), including nine species new to the region and one new species for Peru. For each species, the general distribution is mentioned.

SPECIES ACCOUNTS

ORDER CHIROPTERA

Family Emballonuridae Gervais, 1855

***Peropteryx macrotis* (Wagner, 1843)**

Distribution This species has a wide distribution from southern Mexico south to Bolivia and Paraguay (Hood & Gardner, 2007).

Specimens Examined (1) IQUITOS: Iquitos, Edificio EsSalud (calles Raymondi-Napo), 1 female (MMD 4875).

Additional Records Puerto Indiana, Amazon River (not examined), collected in 1926 by Olalla and sons, and deposited at the American Museum of Natural History (AMNH), New York.

Remarks The only specimen was collected in downtown Iquitos near dusk, at 6:00 pm on the 5th of July 2005, in a mist net placed in the 10th floor of a building. It was a pregnant female with a fetus of Crown Rump (CR) length of 12 mm. In the same building, several specimens of *Myotis albescens* and *Molossus coibensis* were collected.

This species is distributed throughout the Peruvian Amazon. Although previously there were no specimens cited from the town of Iquitos, its presence was probable, as mentioned by Hice et al (2004) for the Reserva Nacional Allpahuayo-Mishana.

The measurements of the specimen from Iquitos (Tab. 1) are in the upper limits for the species, compared with the measurements given by Sanborn (1937), Goodwin & Greenhall (1961), and Willig (1983).

***Peropteryx pallidoptera* Lim et al, 2010**

Distribution This species was recently described by Lim et al (2010) and was known only from three localities in Ecuador and Peru.

Specimens Examined (5) SAN JUAN: Camino a El Paujil, 1.8 km al W del km 35 de la carretera Iquitos-Nauta, 5 females (MMD 3530, 3531, 3532, 3533, 3534).

Remarks This species was found in primary lowland forests and all the specimens from Peru, cited by Lim et al (2010), were captured in their roosts. They were long ago deposited in collections; the one from Orosa was collected in 1926 by the Olalla brothers and was deposited at the AMNH. The 17 specimens from the second locality in Peru (Río Gálvez) were collected in 1998 and 1999, and later deposited at AMNH and at the MHNSM, Lima, Peru, evidencing the similarity of this species with the other "transparent wings *Peropteryx*" (*P. leucoptera*).

The specimens indicated here in "Specimens Examined" were also collected during the day in their roosts on the 13th of July 2004 in a primary forest (but close to a deforested area). This new record represents the third locality for the distribution of the species in Peru and is located about 160 km equidistant from the other two localities. All of the specimens were females and there were four adults and one juvenile. The adults had large mammae and two of them were pregnant, one with two fetuses (CR = 7 mm) and the other with a single embryo (CR = 7 mm). Females generally give birth to a single offspring (Yee, 2000).

The roost was a large cavity on the ground, transversed by many roots of several trees, and was probably excavated by the effects of water (e.g., erosion; Fig. 2). The roost was shared with a male specimen of *Carollia brevicauda*.

The most outstanding characters of *P. pallidoptera*

Tab. 1 External and cranial measurements (acronyms are explained in Materials and Methods). The measurements, or ranges for each measurement, are shown, and then the number of specimens examined (in parentheses) is indicated

	Peropteryx macrotis	*Peropteryx pallidoptera*	*Anoura caudifer*	*Lionycteris spurrelli*	*Vampyrum spectrum*	*Thyroptera lavali*	*Cynomops planirostris*	*Eumops delticus*	*Eumops maurus*	*Molossus coibensis*
ToL	67 (1)	60–65 (4)	65 (1)	70 (1)	147–148 (2)	75 (1)	81–83 (3)	110 (1)	122 (1)	90–109 (15)
TL	15 (1)	11–13 (4)	5 (1)	7 (1)	0 (2)	30 (1)	26–27 (3)	45 (1)	49 (1)	27–40 (15)
HFL	10 (1)	8–9 (4)	12 (1)	11 (1)	30–31 (2)	5 (1)	8–9 (3)	10 (1)	12 (1)	10–12 (15)
EL	17 (1)	14–15 (4)	14 (1)	13 (1)	42–45 (2)	14 (1)	14–15 (3)	22 (1)	22 (1)	12–14 (15)
W	6.75 (1)	4.75–6 (4)	9 (1)	7 (1)	158–182 (2)	5 (1)	9.00–10.25 (3)	14.75 (1)	24 (1)	11.50–21.00 (15)
FA	46.31 (1)	40.21–42.75 (4)	35.29 (1)	34.83 (1)	114.40–118.22 (2)	39 (1)	30.51–31.77 (3)	47.68 (1)	55.45 (1)	34.54–37.70 (15)
GLS	14.54 (1)	13.46–13.97 (2)	21.31 (1)	19.82 (1)	–	15.43 (1)	15.59 (1)	18.38 (1)	19.97 (1)	15.41–16.44 (3)
CIL	13.47 (1)	12.47–12.86 (2)	20.97 (1)	18.31 (1)	–	15.03 (1)	14.85 (1)	18.11 (1)	18.94 (1)	14.42–15.15 (3)
BB	6.79 (1)	6.46–6.76 (2)	8.80 (1)	8.81 (1)	–	7.16 (1)	8.40 (1)	8.78 (1)	10.52 (1)	8.40–9.62 (3)
LIB	4.63 (1)	4.75 (1)	4.62 (1)	3.7 (1)	–	4.42 (1)		6.25 (1)		
PC	3.04 (1)	2.87–2.91 (2)	4.65 (1)	3.91 (1)	–	2.96 (1)	4.18 (1)	4.42 (1)	4.27 (1)	3.96–3.97 (3)
ZB	8.45 (1)	8.13–8.63 (2)	9.60 (1)	8.62 (1)	–	8.01 (1)	10.32 (1)	11.08 (1)	12.44 (1)	10.56–10.80 (3)
MB	7.47 (1)	7.14–7.45 (2)	9.32 (1)	8.04 (1)	–	6.99 (1)	9.16 (1)	10.17 (1)	10.99 (1)	9.45–10.26 3
PL	4.38 (1)	4.30–4.39 (2)	11.82 (1)	8.86 (1)	–	7.49 (1)	6.74 (1)	7.13 (1)	8.12 (1)	4.70–5.24 (3)
MXTL	5.53 (1)	5.08–5.22 (2)	8.23 (1)	6.57 (1)	–	6.47 (1)	5.78 (1)	6.93 (1)	7.63 (1)	5.69–6.00 (3)
M-M	6.18 (1)	5.93–6.59 (2)	5.77 (1)	5.32 (1)	–	5.72 (1)	6.84 (1)	7.67 (1)	8.32 (1)	7.56–7.96 (3)
C-C	3.86 (1)	3.61–3.71 (2)	3.71 (1)	3.22 (1)	–	3.01 (1)	4.21 (1)	4.42 (1)	5 (1)	4.23–4.39 (3)
LM	9.69 (1)	8.76–9.13 (1)	15.65 (1)	13.21 (1)	–	12.03 (1)	11.66 (1)	13.18 (1)	15.16 (1)	11.27–11.95 (3)
LMdT	5.54 (1)	5.04–5.38 (2)	8.71 (1)	7.02 (1)	–	6.60 (1)	6.27 (1)	7.79 (1)	8.26 (1)	6.33–6.72 (3)

are their pale wings (Fig. 3), separated ears, and the first small peg-like upper premolar; the species can be distinguished from *P. leucoptera* by the ears connected by a band, from *P. macrotis* by the color of the wings, and from these two by the first upper molar, which is larger and with an accessory cusp.

Fig. 2 Roost of *Peropteryx pallidoptera*; the arrow points to one of the specimens

Fig. 3 Individual of *Peropteryx pallidoptera* collected at the locality "Camino a El Paujil, 1.8 km al W del km 35 de la carretera Iquitos-Nauta (San Juan)". Photo M. M. Díaz.

Family Phyllostomidae Gray, 1825

Subfamily Glossophaginae Bonaparte, 1845

***Anoura caudifer* (É. Geoffroy Saint-Hilaire, 1818)**

Distribution *Anoura caudifer* is distributed throughout South America in Colombia, Venezuela, Guyana, Surinam, French Guiana, Brazil, Ecuador, Peru, Bolivia, Paraguay, and northern Argentina; its distribution forms a large arc surrounding the central Amazon Basin (Griffiths & Gardner, 2007a).

Specimens Examined (1) SAN JUAN: El Dorado, km 25 de la carretera Iquitos-Nauta, app. 1.5 km al E, 1 male (CML 7557).

Additional records Six specimens from Quebrada Orán, ca. 5 km N Río Amazonas, 85 km NE Iquitos, collected in 1984, are deposited in the Louisiana Museum of Natural History, United States of America. The specimen from San Juan represents the nearest locality to the town of Iquitos, where the species was collected.

Remarks After three years of intensive surveys, only one specimen was captured (in an ecotone between secondary forest and a deforested area) indicating that the abundance of this species is very low in the region. The specimen was an adult male, captured on July 14th 2003 at 10:00 PM during a full moon. At the same mist net, but early in the evening (before moonrise), *Saccopteryx leptura* and *Artibeus* (*Dermanura*) *gnomus* were also captured. The specimen of *Anoura caudifer* from San Juan is compared here with the recently described species *A. cadenoi*, and *A. aequatoris* because of the similarity between them. The presence of a tail, and the upper canines without longitudinal sulcus, separate *A. caudifer* from *A. cadenoi*. If compared with *A. aequatoris*, the uropatagium is less furred (see fig. 4b in Mantilla-Meluk & Baker, 2006). The measurements of this specimen (Tab. 1) match perfectly with those recorded by Mantilla-Meluk & Baker (2006) for *A. caudifer*, except for the foot, perhaps reflecting different ways to take the measure.

Subfamily Lonchophyllinae Griffiths, 1982

***Lionycteris spurrelli* Thomas, 1913**

Distribution This species is known from eastern Panama into central Peru and northern Brazil (Griffiths & Gardner, 2007b).

Specimens Examined (1) SAN JUAN: app. 500 m E km 28.8 de la carretera Iquitos-Nauta, 1 male (MMD 4560).

Remarks This species was previously known from central and southeastern Peru, in Huanuco, Pasco and Cusco departments (Griffiths & Gardner, 2007b). It is here added to the Loreto Department in northeastern Peru. This species is similar to the sympatric *Lonchophylla thomasi*, but *Lionycteris* has a shorter rostrum than any species of *Lonchophylla*; it is even shorter than the braincase. In *Lionycteris*, the upper third and fourth premolars are short and triangular, while the lower third and fourth premolars are trident with the main cusp high and robust (Woodman & Timm, 2006; Griffiths & Gardner, 2007b). The measurements of this specimen coincide with those given by Woodman & Timm (2006).

Fig. 4 Individual of *Eumops maurus* collected at the locality "Asociación de Viviendas 15 de Mayo (San Juan)". Photo M. M. Díaz.

The only specimen was collected on April 13th 2005 at 10:00 pm, in a mist net set at ground level in primary forest. Other species collected in the same locality were *Artibeus obscurus*, *Carollia brevicauda*, *C. perspicillata*, *Carollia* sp. ("*castanea* group"), *Mesophylla macconnelli*, *Rhynophylla fisherae*, *R. pumilio*, *Sturnira lilium*, *S. tildae*, *Vampyressa thyone*, and *Myotis riparius*.

Subfamily Phyllostominae Gray, 1825

***Vampyrum spectrum* (Linnaeus, 1758)**

Distribution This species is distributed from Mexico to South America, where it is found in Colombia, Venezuela, Trinidad, Surinam, French Guiana, Ecuador, Brazil, Peru, and Bolivia (Williams & Genoways, 2007).

Specimens Examined (2) SAN JUAN: 1 km E km 25.3 de la carretera Iquitos-Nauta (Fundo San Martín), 1 female (CML 7558); km 25 de la carretera Iquitos-Nauta (Fundo San Martín), 1 female (MMD 5137).

Remarks The two specimens were collected in secondary forest habitat, on May 25th and December 11th 2006; both were adult females with closed vaginas. Twenty-six other species of bats (Emballonuridae, Phyllostomidae, and Vespertilionidae) were collected in the same area. The nearest locality where this species has been previously collected (with voucher specimens) is at Yarinacocha (Ucayali), more than 500 km SW of Iquitos, as cited by Sanborn (1949). Recently Klingbeil & Willig (2009) have mentioned the presence of this species in their study area in southwestern Iquitos, but no voucher specimens, nor a specific locality, were indicated by the authors.

Family Thyropteridae Miller, 1907

***Thyroptera lavali* Pine, 1993**

Distribution This species has been recorded in Peru, Brazil, Ecuador, and Venezuela (Wilson, 2007).

Specimens Examined (1) SAN JUAN: Zungarococha, 5.4 km al W del km 6 de la carretera Iquitos-Nauta, 1 female (MMD 716).

Remarks The only captured specimen represents the first report of the species for Iquitos, and the northernmost record for Peru. The closest known records are the type locality (Quebrada Esperanza, near the Brazilian border) (Pine, 1993) and Jenaro Herrera (Ascorra et al, 1993) (but cited as *T. discifera* and later re-identified as *T. lavali* by Solari et al, 2004). Both the characters and the measurements of this specimen correspond with the original description of the species (see Pine, 1993), except for the ear length, which is given as 8 mm in Pine (1993) but is 14 mm in this study. However, Reid et al (2000) indicates a range of 11−13 mm for *T. lavali*. The specimen from Iquitos was an adult female with a closed vagina. It was collected on December 18th 2002, at 7:00 pm, on a clear and cloudless night with a full moon, in a ground level mist net placed in secondary forest, together with *Carollia perspicillata*, *Lophostoma silvicolum*, and *Artibeus* (*Dermanura*) *anderseni*.

Family Molossidae Gervais, 1856

***Cynomops planirostris* (Peters, 1866)**

Distribution This species is found east of the Andes in South America, from Colombia, Venezuela, and the Guianas, south through Peru and Bolivia, and into Paraguay and Argentina (Eger, 2007).

Specimens Examined (3) PUNCHANA: Villa del Ejército (entre Av. 28 Julio-Freyre y calle Piura), 3 females (2 MMD 5010, 5011, 1 CML 7561).

Remarks Although this species has a widespread distribution, there were previously no records for northeastern Peru. The species of *Cynomops* recorded for the area were *Cynomops abrasus*, *C. milleri*, and *C. paranus* (Eger, 2007).

The three specimens examined were collected in an urban area on September 20th, 2005, at 6:30 pm, during a warm and misty night with a full moon. The specimens were trapped in mist nets elevated 2 m above the ground. All were females with developed mammae; one was pregnant with a single fetus of CR=16 mm.

***Eumops delticus* Thomas, 1923**

Distribution The distribution of this species was known from southeastern Colombia and along the Amazon River in Brazil (Eger, 2007). It is here included in Peru.

Specimens Examined (1) SAN JUAN: Piscina Olímpica del Instituto Peruano de Deportes, km 1.5 al W de la carretera Iquitos-Nauta, 1 female (CML 7560).

Remarks *Eumops delticus* was treated as a subspecies of *E. bonariensis* (see Eger, 1977; Simmons, 2005). However Eger (2007), later decided to revalidate its specific level and restrict the distribution of *E. bonariensis* to southern South America, in Brazil, Uruguay, and Argentina. During this study, only one specimen was collected in five years of surveys; this specimen represents the first record of this species for the country. The specimen was a pregnant female, with a fetus of CR=20 mm, collected at 6:30 pm on 9th October 2003. The collecting locality is close to the town of Iquitos in a recreational area. The specimen was captured in an elevated net set between a few palm trees and a swimming pool. *Molossus molossus* was the only other species collected at this location.

***Eumops maurus* (Thomas, 1901)**

Distribution This rare species is known from only a few specimens and localities (see Eger 2007) from Guyana, Surinam, Venezuela, Ecuador (Tirira, 2006; Eger, 2007), and Peru (Luna et al, 2002).

Specimens Examined (1) SAN JUAN: Asociación de Viviendas 15 de Mayo (E Av. Quiñones), 1 female (CML 7559).

Remarks This record widely extends the distribution of this species in Peru and represents the second locality in the country. It was previously known from the Pampas del Heath, Madre de Dios (Pacheco et al, 2009), about 1000 km south of the present record. The specimen was a pregnant female with a CR=27 mm fetus, captured at 7:30 pm on July 4th, 2005, on a hot day with a clear sky, in a net elevated about 2 m above the ground. The habitat was a suburban area, with a few houses, grasses, flooded grasslands ("gramalotal"), and some yucca plants (manioc), all surrounded by secondary forests. The characters of this specimen are the typical for the species, including a band of white hairs on the ventral surface of the mesopatagium, next to body (Fig. 4). However, the forearm (55.45 mm) is slightly larger than the average for the few known specimens of this species. Other species captured at the same locality were *Carollia perspicillata*, *Platyrrhinus brachycephalus*, and *Uroderma magnirostrum*.

Molossus coibensis **J. A. Allen, 1904**

Distribution In South America, this species is known from eastern Colombia, Peru, Ecuador, Venezuela, Guyana, French Guiana, and west-central Brazil (Eger, 2007).

Specimens Examined (15) BELEN: Moena Caño, 3 females (MMD 2602, 2604, 2611) and 2 males (MMD 2603, 2625). IQUITOS Colegio Primario Secundario "RADM" (Rosa Agustina Donayre de Morey), calle Putumayo, 3 females (MMD 4336, 4337, 4341) and 1 male (CML 7562); Iquitos, Edificio EsSalud (calles Raymondi-Napo), 4 females (MMD 4864, 4873, 4876, 4878). PUNCHANA: Punchana, Calle Amazonas 1086 (casa de Dr. Gendrau), 1 female (CML 7563) and 1 male (MMD 3124).

Remarks *M. coibensis* was previously considered as a synonym of *M. molossus* by Koopman (1993), but recently several authors (e.g., Reid et al, 2000; Simmons, 2005; Eger, 2007), following Dolan (1989), began to treat it as a valid species. Both species are similar, but *M. coibensis* is smaller and the dorsal pelage is shorter and practically unicolored, with a shorter white basal band of hairs and shorter and spatulated upper incisors.

Certainly, many of the specimens from Peru that are identified in the literature as *Molossus molossus* may belong to this species. It is therefore essential to review these specimens to more accurately determine the distribution of this species in the country. However, there was a previous record of this species from Huanuco Department, in central Peru, south of the region of Iquitos (Eger, 2007). In Iquitos, most of the specimens were netted in urban areas. In a downtown building (Edificio EsSalud), the specimens were captured in a net placed in the 10th floor, where specimens of *Myotis albescens* and *P. macrotis* were also captured. Two other specimens were collected in the roof of a house where they were roosting with several specimens of *M. molossus*. All other specimens were captured in a school, along with *M. molossus*, *M. rufus* and *Phyllostomus hastatus*. Only the specimens from Moena Caño were captured in a natural habitat, a secondary forest area, with elevated mist nets during the evening. At least 15 other species belonging to four families (Emballonuridae, Molossidae, Phyllostomidae, and Vespertilionidae) were also collected in this locality. Pregnant females were recorded on 24th November 2003, 24th March 2004, 3rd March 2005, and 5th July 2005, and a male with scrotal testicles was registered on 25th November 2003.

3 Discussion

The small mammals of the Amazon Basin of Peru have been the subject of numerous studies, but the attention has mainly focused on the southern and central parts of the country, particularly the Manu area (Terborgh et al, 1984; Janson & Emmons, 1990; Ascorra et al, 1991, 1996; Patterson et al, 1992, 1996, 1998, 2006; Pacheco et al, 1993, 1994; Pacheco & Vivar, 1996; Wilson & Sandoval, 1996; Zeballos-Patrón et al, 2001; Leite-Pitman et al, 2003; Bravo et al, 2008). Only a few studies have been conducted in the northeastern area (Sandborn, 1949; Thomas, 1924, 1927, 1928a, b; Ascorra et al, 1993), and specifically in Iquitos, including by members of our research group and colleagues (Davis & Dixon, 1976; Hice, 2003; Angulo & Díaz, 2004; Díaz & Willig, 2004; Hice et al, 2004; Willig et al, 2007). However, none of these investigations has included sampling in urban and suburban areas. As a consequence, my decision to include these areas in our surveys has resulted in the collection of several species recorded for the first time, as well as species newly added to the region and to the country.

Despite intensive sampling over several years, all of these new distributional records were obtained by capturing just a few specimens. Only single specimens were captured for *A. caudifer*, *L. spurrelli*, *P. macrotis*, *E. delticus*, and *E. maurus*. Two specimens of *V. spectrum* and three of *C. planirostris* were obtained, and five specimens of *Peropteryx pallidoptera* were captured from the roost at one locality. This reflects the low abundance of these species and indicates their rarity. *Molossus coibensis*, a widely distributed and very abundant species, was the only of the new species collected in this study that has been recorded by several specimens. *Lionycteris spurelli* and *Peropteryx pallidoptera* were the only specimens collected in primary forest, a habitat where both species are frequently related (Handley, 1976; Lim et al, 2010). All other species were collected in somewhat modified environments, such as rural areas (*Eumops delticus*), suburban areas (*Eumops maurus*), secondary forest-deforested ecotones (*Anoura caudifer*), secondary forests (*Molossus coibensis*, *Thyroptera lavali* and *Vampyrum spectrum*), and urban areas (*Peropteryx microtis*, *Cynomops planirostris* and *Molossus coibensis*).

The presence of *T. lavali* in secondary forests was not known, and some authors (Reid et al, 2000; Solari et al, 2004) have indicated that "it seems to prefer primary forest near swamps". In this study, the species was collected in a secondary forest patch surrounded by agricultural fields and flooded areas. *A. caudifer* and *V. spectrum* were captured in secondary forests but these localities were surrounded by very large patches of well-preserved forests. For example, *V. spectrum* was captured in a locality close to the wildlife reserve of Allpahuayo Mishana. The presence of molossid bats in urban and suburban areas is well known; moreover, the presence of emballonurids in these environments is apparently more common than supposed. Several distributional range extensions and inclusions of new species in some countries were consequences of specimens collected in urban areas (Handley, 1976; Furlonger et al, 1987; Sodré & Uiedam, 2006; Dalponte & Aguiar, 2009; Mantilla-Meluk et al, 2009). It is possible that those specimens were attracted by roosting opportunities in buildings, or by the insects flying around the nearby street lamps (Dalponte & Aguiar, 2009).

It is well known that habitat modification for agricultural purposes (Aramburú, 1984; Hice, 2003; Willig et al, 2007) is one of the greatest threats to nature. This process has a negative effect on biodiversity, mainly because of the isolation imposed on environments and the resulting decrease in species richness and modification of population dynamics (Luque et al, 1994; Iida & Nakashizuka, 1995; Luque, 2000).

Habitat destruction, deforestation due to population pressure, the use of wood, and the exploitation of land for agricultural purposes were all observed during this study. In this context, it is necessary to state that bats are one of the groups of mammals most affected by habitat destruction and fragmentation (Cosson et al, 1999; Gorresen & Willig, 2004). The Iquitos region in particular, is a very distressed and fragmented area (Willig et al, 2007) and is included in the Peruvian Amazon forest, where approximately 0.4% (271,000 ha) is being converted to cropland or pasture each year (World Resources Institute, 1990).

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Appendix I

List of localities, district and province in brackets, geographic coordinates, and type of habitat.

1. 1 km E km 25.3 de la carretera Iquitos-Nauta (Fundo San Martín) (San Juan) 3º 57.954' S 73º 24.259' W—Tropical humid forest.
2. app. 500 m E km 28.8 de la carretera Iquitos-Nauta (San Juan) 3º 59.227' S 73º 24.920' W—Tropical humid forest.
3. Asociación de Viviendas 15 de Mayo (E Av. Quiñones) (San Juan) 3° 45.903' S 73° 17.725' W—Suburban area.
4. Camino a El Paujil, 1,8 km al W del km 35 de la carretera Iquitos-Nauta (San Juan) 4° 01.217' S 73° 26.787' W—Tropical humid forest.
5. Colegio Primario Secundario "RADM" (Rosa Agustina Donayre de Morey), calle Putumayo (Iquitos) 3° 44.997' S 73° 15.137' W—Urban area.
6. El Dorado, km 25 de la carretera Iquitos-Nauta, app. 1.5 km al E (San Juan) 3º 58.010' S 73º 23.620' W—Ecotone deforested area and secondary forest.
7. Iquitos, Edificio EsSalud (calles Raymondi-Napo) (Iquitos) 3° 44.942' S 73° 14.613' W—Urban area.
8. km 25 de la carretera Iquitos-Nauta (Fundo San Martín) (San Juan) 3º 57.954' S 73º 24.259' W—Secondary forest.
9. Moena Caño (Belén) 3º 46.728' S 73º 13.495' W—Secondary forest.
10. Piscina Olímpica del Instituto Peruano de Deportes, km 1.5 al W de la carretera Iquitos-Nauta (San Juan) 3° 47.696' S 73° 18.231' W—Rural area.
11. Puerto Indiana, Amazon River (Indiana) 03° 43.05' S 73° 04.32' W.
12. Punchana, Calle Amazonas 1086 (casa de Dr. Gendrau) (Punchana) 3° 43.506' S 73° 15.113' W—Urban area.
13. Villa del Ejército (entre Av. 28 de Julio-Freyre y calle Piura) (Punchana) 3° 43.658' S 73° 14.608' W—Urban area.
14. Zungarococha, 5.4 km al W del km 6 de la carretera Iquitos-Nauta (San Juan) 3° 49.825' S 73° 22.288' W—Secondary forest.

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新疆草兔的种群遗传结构和亚种分化

BACK

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摘要：新疆草兔 (*Lepus capensis*) 的群体遗传结构至今无系统的研究报道，亚种水平的分类也长期存在争议。该文测定了形态分类上的新疆草兔3个亚种共87个个体的线粒体DNA (mtDNA)控制区(control region, D-Loop)592 bp的序列，经分析发现148个多态性位点，共定义了44个单倍型。新疆草兔的单倍型多样度(h，0.977 ± 0.005)和核苷酸多样度(π，0.064 ± 0.031)都较高，显示了较高的遗传多样性。分子变异分析(AMOVA)结果显示，4个地理群体间的显著分化可能是由地理隔离造成的。群体遗传结构分析显示，新疆草兔包含 4 个进化枝，并且每个进化枝都对应特定的分布区域，显示了明显的系统地理结构。该研究的结果支持形态分类上草兔西域亚种(*L.c. lehmanni*)的分类地位；但中亚亚种(*L.c. centrasiaticus*)被分为两个独立的进化枝，提示可能存在两个亚种；帕米尔亚种(*L.c. pamirensis*)与其他亚种间的遗传距离在13%以上，提示其可能已达到种的分化水平。

关键词：草兔；线粒体DNA；控制区；群体遗传多样性；亚种分化
中图分类号：Q959.836; Q349.1 **文献标志码**：A **文章编号**：0254-5853-(2011)02-0179-09

Genetic structure and subspecies divergence of *Lepus capensis* in Xinjiang

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Abstract: To date, the genetic structure and genetic diversity of *Lepus capensis* in Xinjiang has not been systematically studied at the molecular level, and its subspecies taxonomic status has been under debate for years. According to traditional morphology, there are three subspecies of *L. capensis* distributed in Xinjiang: *L.c. centrasiaticus*, *L.c. lehmanni* and *L.c. pamirensis.* In this study, we determined 592 bp D-loop sequences of 87 cape hares from Xinjiang Province. Forty-four haplotypes were defined based on 148 polymorphic sites. Both the haplotype diversity (0.977 ± 0.005) and nucleotide diversity (0.064 ± 0.031) are high. F_{ST} P values are significantly high and no haplotype was shared among the four geographic populations, indicating that genetic differentiation among populations is significant. AMOVA shows that most of the genetic differentiation occurred among geographic groups, indicating that geographic isolation such as mountains and deserts might make an effective barrier against gene flow. Both the phylogenetic tree and median-joining network grouped 44 haplotypes into four distinct clades corresponding to four geographic areas, indicating an obvious phylogeographic pattern. Our data supported the subspecies status of *L. c. lehmanni*. The fact that haplotypes of *L. c. centrasiaticus* were grouped into two distinct clades suggests that this traditional subspecies should be considered as two subspecies. In addition, *L. c. pamirensis* shows a significantly higher sequence divergence compared to other subspecies, and the difference even reached the level of species.

Key words: *Lepus capensis*; mtDNA; Control region; Genetic structure; Subspecies

草兔 (*Lepus capensis*)是世界上分布范围最广的兔属物种之一，广泛分布于非洲、中东、中亚，甚至太平洋沿岸(Hichem et al, 2008; Flux & Angermann, 1990; Hoffmann & Smith, 2005; Chapman

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& Flux, 2008)。在我国分布于东北、华北、西北和长江中下游地区。由于草兔在全世界分布较广，分布在不同地理区域的个体表现出对栖息地环境的适应性而具有不同的形态特征，以及分布区重叠等使其亚种的划分到现在都没有澄清(Chapman & Flux, 2008)。

Luo(1988)对中国野兔的形态分类进行的系统研究指出，中国草兔可分为 8 个亚种，其中新疆分布有 3 个亚种，分别为分布在东疆、吐鲁番盆地、焉耆盆地的中亚亚种(*L.c.centrasiaticus*)；分布在乌鲁木齐以西、塔里木盆地以北广大地区的西域亚种(*L.c.lehmanni*)；分布在帕米尔高原塔什库尔干的帕米尔亚种(*L.c.pamirensis*)。Wang(2003)得出一致观点，但将中亚亚种和西域亚种分别称为甘肃亚种(*L.c.centrasiaticus*)和哈萨克亚种(*L.c.lehmanni*)。然而，由于新疆地域辽阔，高大山脉与平原交错分布，绿洲、农牧与沙漠戈壁相间排列，并且在新疆分布的这 3 个亚种之间被广阔的沙漠和山脉隔开，使得草兔生存环境呈现出复杂的多样性。另外，传统上针对新疆草兔的研究涉及的样品数量较少，缺乏广泛的取样，而且目前尚无分子方面系统的研究报道。

Wu et al(2005)应用 4 个线粒体基因对中国 9 种野兔的系统发育进行了研究，并提示新疆可能存在两个以上的野兔新种，但是该项研究仅仅包含了 3 个来自新疆的样品。在新疆境内，雪兔和塔里木兔都具有比较集中的分布区域和特有的形态特征(Luo, 1988; Wang, 2003; Andrew & Yan, 2008)。因此，在这两个物种的分布区域内存在新种的可能性较小，而新疆草兔的分布区域较广，环境多样，最有可能存在尚未发现的兔属物种。

从草兔在世界范围内的广泛分布来看，它应该是进化最成功、适应性最强的兔属物种，因此，弄清草兔的群体历史和遗传结构对于理解整个兔属物种的进化历史具有重要的参考价值。线粒体 DNA 控制区由于进化速度快、变异位点多，可以将近期分歧谱系区分开来。因此，是一种探讨种内遗传结构、种群差异与生物地理关系等的有效遗传标记(Avise, 1992; Van et al, 2002; Yang et al, 2008)。本研究的目的就是通过测定新疆草兔线粒体 DNA 控制区序列，结合系统发育和群体遗传学的分析方法来了解新疆草兔的群体遗传多样性和遗传结构，利用多层次分子变异分析探讨山脉和沙漠戈壁等对草兔种群遗传结构的影响；结合传统形态学的观点进一步探讨新疆草兔的亚种分化问题以及是否存在新种。

1 材料和方法

1.1 样品收集及采样点区域划分

本研究共收集到 87 个新疆草兔样品。样本采集地基本覆盖了新疆草兔分布区域(Luo, 1988; Wang, 2003)。在新疆草兔亚种分类的基础上，结合新疆的山脉和沙漠戈壁等地貌特征，将上述样品分为 4 大分布区域，作为数据分析中的地理种群。样品详细信息和分布图见表 1 和图 1。其中南部和东部种群的草兔分别属于帕米尔亚种和中亚亚种，北部和西部种群的草兔属于西域亚种。

表 1 本研究的样品信息

Tab. 1 Specimens examined in this study

亚种 Subspecies	种群 Population	采集地 Sites	样品数 Sample size	经度 Latitude	纬度 Longitude
西域亚种 *L.c.lehmanni*	北部 North	福海 Fuhai, FH	20	87.51	47.15
		青河 Qinggil, QH	2	90.37	46.71
		阿勒泰 Altay, ALT	1	88.14	47.86
		哈巴河 Habahe, HBH	4	86.41	48.05
		布尔津 Burqin, BRJ	2	86.92	47.70
		富蕴 Fuyun, FY	3	89.44	47.05
	西部 West	精河 Jinghe, JH	26	82.92	44.67
		温泉 Wenquan, WQ	1	81.08	44.95
中亚亚种 *L.c.centrasiaticus*	东部 East	哈密 Hami, HM	12	93.44	42.78
		博湖 Bohu, BH	3	86.53	41.95
帕米尔亚种 *L.c.pamirensis*	南部 South	塔什库尔干县 Taxkorgan, TX	13	75.22	37.76

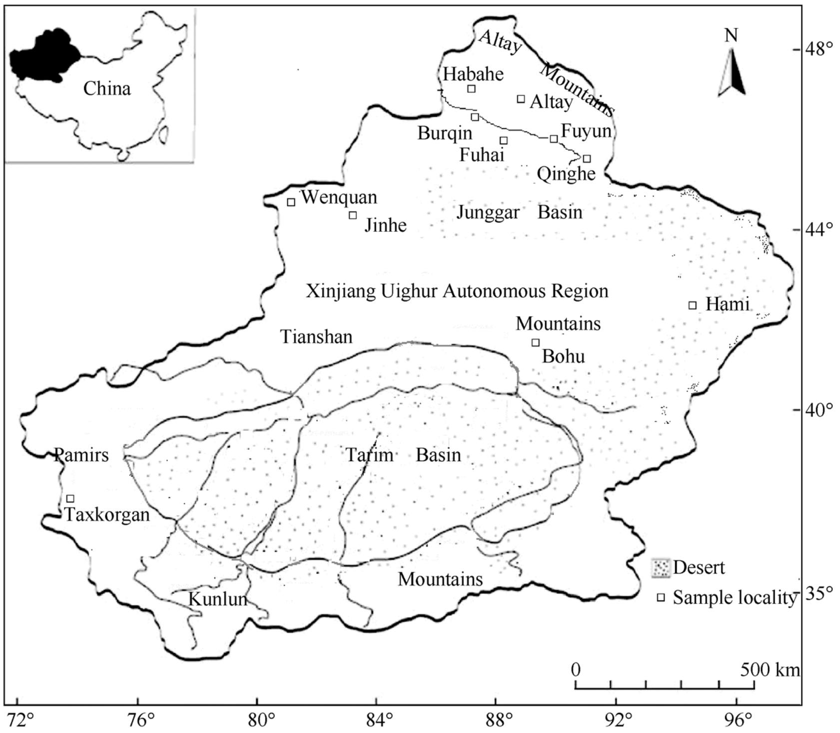

图 1　本研究所用样品的地理分布

Fig. 1　Approximate geographical distribution of DNA samples in this study

1.2　总 DNA 提取

本研究所收集的样品包括肌肉组织、新鲜毛皮及陈旧皮张样品，采用经典的酚–氯仿方法提取(Sambrook et al, 1989)：取适量组织，加蛋白酶 K 消化过夜，然后依次用饱和酚∶氯仿∶异戊醇(25∶24∶1)和氯仿∶异戊醇(24∶1)分别抽提 2 次，再用无水乙醇沉淀和 70%的乙醇洗涤，离心甩干，最后溶于 TE 中。

1.3　PCR 扩增

引物设计基于已发表的穴兔及其他一些兔属动物线粒体DNA序列(Gissi et al, 1998; Conrad et al, 2004)，本研究所用引物为 5' -cat gca tat aag cca gta-3', 5' -atg cat ggg gat aag gtt tt-3'。PCR 反应条件为 94 ℃ 1 min, 55 ℃ 1 min, 72 ℃ 1 min 35 个循环。最后 72 ℃延伸 5～10 min。PCR 产物经凝胶电泳用上海华舜生物工程有限公司的小量胶回收纯化试剂盒进行纯化。纯化后得到的 PCR 产物直接作为模板，使用 PE 公司的 BigDye^{TM} Terminator Kit (V2.0)，根据厂家推荐的条件进行测序反应。测序反应产物经纯化后，使用 Applied Biosystems Inc.的 3730 全自动 DNA 序列仪电泳并由机器自动记录序列数据。每条序列均经过正反链双向测定，以确保序列的准确性。

1.4　数据分析

用 DNAstar5.0 软件包中的 Editseq 和 Seqman 子程序进行基因片段的拼接合并，用 ClustalW1.83(Thompson et al, 1997)排序。运用 MEGA 4 软件(Tamura et al, 2007)进行序列特征分析，计算成对遗传距离(p-distance)。运用 GenAlEx 软件(Peakall & Smouse, 2007)计算地理距离与遗传距离之间的相关性(Mantel tests)。运用 Network4.1.1.2 软件(Bandelt et al, 1999)(http://www.fluxux-engineering.com)构建草兔种群的中介网络图(median-joining network)。运用 Arlequin3.1 (Excoffier & Laval, 2005)(http://cmpg.unibe.ch/software/arlequin3)软件计算单倍型多样度(haplotype diversity, *h*)、核苷酸多样度(nucleotide diversity, π)、基于各种群间的遗传分化指标 F-Statistics(F_{ST})值以及进行分子变异分析(analysis of molecular variance, AMOVA)(Excoffier et al, 1992)、核苷酸错配分布(mismatch distribution)分析和包括 Tajima’s D 值(Tajima, 1989)、Fu 的 *Fs* 值(Fu, 1997)及其 *P*-value 在内的中性检验分析(neutrality tests)。

系统树的构建采用邻接法——neighbor-joining, NJ(Saitou & Nei, 1987)和贝叶斯方法(Huelsenbeck & Ronquist, 2001), 以穴兔(*Oryctolagus cuniculus*)和海南兔(*Lepus hainanus*)作为外群。NJ 树用 MEGA 4 (Tamura et al, 2007)软件构建, 参数均采用默认设置。贝叶斯树用 MrBayes v3.04b (Ronquist & Huelsenbeck, 2003)构建。首先使用 MODELTEST 3.7 (Posada & Crandall, 1998)程序选出 HKY+I+G 作为适合本研究数据的最优核苷酸替换模型, 具体参数为: Base=(0.3116 0.2910 0.0989), Nst=2, Tratio=5.9584, Rates =gamma, Shape =5.9584, Pinvar =0.4160。贝叶斯分析是以随机树开始, 运行 300 万代, 每 100 代取样一次。在同样设置的参数下, 我们运行两次。用于构建主要一致树的后验概率分布, 是预先舍弃了似然率差异较大的前 7 500 次取样(Leaché & Reeder, 2002)。

2 结果与分析

2.1 新疆草兔 mtDNA D-1oop 区的序列特征

在 87 条草兔 mtDNA D-loop 区 592 bp 的序列中, 共发现 148 个多态性核苷酸位点, 占全部碱基数的 25.08%; 简约信息位点 128 个, 其中转换(transition)26 个、颠换(transversion)6 个、插入/缺失(insertion/deletion)34 个和其他 62 个。将 13 个草兔采集地划分为 4 个地理种群, 序列分析结果表明, 4 个地理种群的 87 个样品中共存在单倍型 44 个(GenBank 序列号为 HQ699901～HQ699944), 其中东部种群 13 个、北部种群 12 个、西部种群 10 个和南部种群 9 个。4 种群间无共享单倍型。

2.2 草兔群体的遗传多样性及遗传结构

2.2.1 Mantel tests 分析 Mantel tests 分析结果(图 2)为: 横轴遗传距离(GD)与纵轴地理距离(GGD)之间呈现明显的相关性, 且 P 值为 0.010, 小于 0.05 的显著水平。草兔各种群之间地理距离越大, 遗传距离也越大。

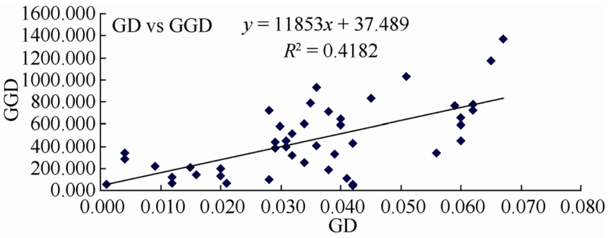

图 2 Mantel tests 分析结果

Fig. 2 Results of Mantel tests analysis

GD: 遗传距离 Genetic distance; GGD: 地理距离 Geographic distance.

2.2.2 遗传多样性 新疆草兔 4 个地理种群中, 东部种群的核苷酸多样度 π 和单倍型多样度 h 最高, 分别为(0.057 ± 0.029)和(0.971 ± 0.039), 北部种群最低, 分别为(0.015 ± 0.008)和(0.901 ± 0.027)。总的来说, 新疆草兔具有较高的遗传多样性[核苷酸多样度(0.064 ± 0.031); 单倍型多样度(0.977 ± 0.005), 见表 2]。新疆草兔群体的 Tajima's D 和 Fu's *Fs* 的中性检验并不显著 (分别为 −1.914 和 1.466, $P >$ 0.05, 见表 2), 核苷酸错配分析显示多峰分布(图未显示)。

表 2 基于草兔 mtDNA D-loop 区计算的遗传多样性及种群动力学参数

Tab. 2 Diversity and demographic parameters deduced from mtDNA D-loop sequences in *lepus capensis*

种群 Population	样品数 Sample size	单倍型数 Number of haplotypes	核苷酸多样度(π) Nucleotide diversity	单倍型多样度(h) Haplotype diversity	Tajima's D	Fu's *Fs*
North	32	12	0.015 ± 0.008	0.901 ± 0.027	−1.914	1.466
West	27	10	0.019 ± 0.010	0.917 ± 0.023	0.585	3.287
East	15	13	0.057 ± 0.029	0.971 ± 0.039	0.892	0.091
South	13	9	0.028 ± 0.015	0.936 ± 0.051	1.090	1.361
总体 Total	**87**	**44**	**0.064 ± 0.031**	**0.977 ± 0.005**	**0.410**	**0.508**

2.2.3 遗传结构 AMOVA 分析显示, 当种群间相距的远近程度和天然地理屏障将新疆草兔划分成不同地理组群时(表 3), 地理组群间的变异, 分别占 58.91%和 68.45%; 将草兔群体各自独立为一组时, 种群间的变异贡献率也较大, 为 44.55%, 且 P 值极显著。

种群间的遗传分化指数 F_{ST} 值(对角线以下)(表 4)分析显示, 新疆草兔各种群间 F_{ST} P 值均小于 0.01 的检验水平, 且南部种群与其它种群间的 F_{ST} 值最大, 其与北部、西部和东部种群的数值分

表 3　新疆草兔 mtDNA 单倍型分子变异等级分析(AMOVA)

Tab. 3　Hierarchical analysis of molecular variance (AMOVA) of mtDNA haplotypes of Cape hare in Xinjiang

分 组 Groups	分化指数 F_{CT}	 F_{SC}	 F_{ST}	组群间 Among groups	组群内各种群间 Among populations within groups	种群内 Within populations
[北西][东][南][N W][E][S]	0.5891	0.3753^*	0.7433^*	58.91	15.42^*	25.67^*
[北西东][南] [N W E] [S]	0.6845	0.4407^*	0.8235^*	68.45	13.91^*	17.65^*
[北][西][东][南][N][W][E][S]	—	—	0.4455^*	—	44.55^*	55.45

$^*P< 0.01$.

别为 0.866、0.849 和 0.703。各种群间的基因交流均很小(均小于 1, 见表 4), 尤其是南部种群与其它 3 个种群之间的基因交流值最小。

表 4　新疆草兔 4 个地理种群的遗传分化指数及基因流

Tab. 4　F_{ST}(below the diagonal)and gene flow(above the diagonal) among the four populations of Cape hare in Xinjiang

种群 Population	北部 North	西部 West	东部 East	南部 South
北部 North		0.54	0.60	0.08
西部 West	0.479^*		0.65	0.09
东部 East	0.456^*	0.436^*		0.21
南部 South	0.866^*	0.849^*	0.703^*	

$^*P< 0.01$.

2.2.4　系统发育关系　NJ 树和贝叶斯树(图 3)显示, 新疆草兔 44 个单倍型被分为支持率较高的 4 个进化枝(Clade A～D), 每个进化枝均包含了绝大部分来自相同或相邻区域的样品, 如 Clade A 包含了绝大多数来自新疆西部和北部种群的单倍型; Clade B 和 D 中的单倍型分别全部来自新疆东部种群和南部种群; Clade C 中的样品主要来自新疆东部群体。虽然地理上相距较远的个别单倍型在进化枝上稍有交叉, 但仍可以看出新疆草兔群体具有明显的系统地理结构。

同时, 我们分析了基于进化树上(图 3)4 个进化枝间的遗传分化指数 F_{ST} 值(对角线以下)和种群间 ML 遗传距离(对角线以上)(表 5), 结果显示, 新疆草兔各进化枝的系群分化十分显著($P<0.01$), Clade D 与其他进化枝间的遗传距离(p-distance)最大, 均达到 13%以上, CladeA、B 和 C 间的遗传距离在 6.5%～7.7%之间。

新疆草兔 mtDNA 控制区 44 个单倍型的中介网络图(图 4)更清晰直观地显示出新疆草兔群体的系统地理结构。与系统发育分析一样, 网络图也明显的将 44 个单倍型分为 4 个进化枝, 其中 Clade D 中

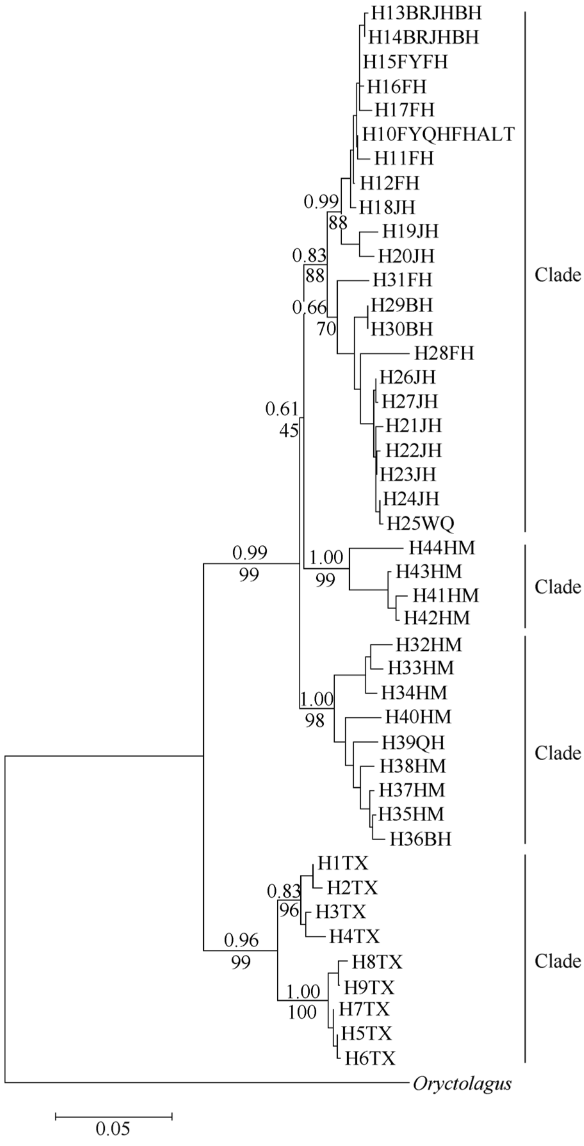

图 3　基于新疆草兔 mtDNA 控制区 44 个单倍型的序列构建的贝叶斯树

Fig. 3　Bayesian inference tree of 44 mtDNA haplotypes based on mtDNA control region fragment of Cape hare in Xinjiang

NJ 树与贝叶斯树的拓扑结构相同; 进化枝上和枝下的数字分别代表贝叶斯树的后验概率和 NJ 树的支持率。

Neighbour-joining tree obtained the same topology with Bayesian tree. Numbers above the branches are Bayesian posterior probabilities and those below the branches are the bootstrap proportions derived from a Neighbour-joining tree.

的单倍型都来自南部群体，且与其他进化枝间的突变步数高达 71 步。来自北部和西部群体的单倍型主要分布在 Clade A 中。来自东部群体的单倍型被分为了两个关系较远的进化枝(Clade B 和 Clade C)。从图中还可以看出，来自新疆西部、北部、中部及东部地区的草兔并没有共享单倍型，所有单倍型均为该地区的独有单倍型。

表 5 新疆草兔 4 个进化枝的系群的遗传分化指数及遗传距离

Tab. 5 F_{ST}(below the diagonal)and genetic distance (above the diagonal) between 4 clades of Cape hare in Xinjiang

	Clade A	Clade B	Clade C	Clade D
Clade A		0.070	0.065	0.130
Clade B	0.690^*		0.077	0.141
Clade C	0.604^*	0.647^*		0.134
Clade D	0.837^*	0.831^*	0.790^*	

$^*P< 0.01$.

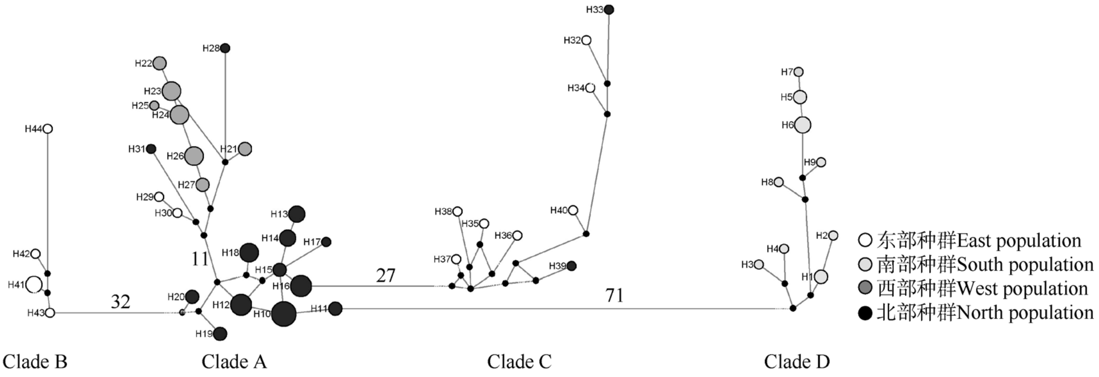

图 4 新疆草兔 mtDNA 控制区 44 个单倍型的中介网络图

Fig. 4 Median-joining network for 44 mtDNA control region haplotypes of *Lepus capensis*

圆圈的面积与单倍型频率成比例，粗体数字代表突变步数（仅显示了主要的突变步骤）。

The area of the circle is proportional to the haplotype frequency. The bold numbers in network represent mutational steps (only primary mutational steps are shown).

3 讨 论

3.1 遗传多样性

相比于其他它已报道的兔属物种，如欧兔(*L. europaeus*)h=0.988±0.004, π =0.027±0.003; 地中海草兔 (*L.c. mediterraneus*) h= 0.870±0.042, π =0.014±0.008; 雪兔 (*L. timidus*) h=0.977±0.027, π =0.057±0.029(Massimo et al, 2003); 塔里木兔 h=0.984 ± 0.004, π =0.045 ± 0.022(Li et al, 2006)。本研究检测到新疆草兔具有较高的遗传多样性(h=0.977 ± 0.005, π=0.064 ± 0.031)。新疆草兔种群较高的遗传多样性可能是由于其存在一个相当大的有效种群(Su et al, 2001)，或野外种群数量较大，其庞大的种群数量能有效地保存群体内的遗传变异。同时，新疆草兔复杂多样的生存环境也会促进其群体分化。新疆草兔群体的 Tajima’s D 和 Fu’s *Fs* 的中性检验并不显著 (分别为 −1.914 和 1.466, $P > 0.05$，见表 2)。核苷酸错配分析显示多峰分布(图未显示)，这主要是由新疆草兔群体存在较为明显的遗传分化而致(系统发育分析显示存在 4 个分化明显的进化枝)，在一些家养动物的群体研究中也发现了类似的现象(He et al, 2008)。另外，第四纪冰期对于兔属物种的形成、扩散和遗传结构也产生了重大的影响(Avise et al, 1998; Hewitt, 1996; Shi et al, 2006)。

3.2 遗传结构

地理隔离是群体间基因交流的天然屏障，是影响群体间遗传分化的重要因素。Wright 的距离隔离(isolation by distance)理论认为，自然界存在着距离隔离现象，即物种遗传分化的程度会随着地理距离的增加而增加(Wright, 1943)，许多研究也证实了这一理论(Floyd et al, 2005; Trizio et al, 2005)。

我们在分析新疆草兔的系统地理结构时，并没有按照形态分类上的亚种分布地来划分草兔群体，而是根据新疆的地形和地理距离划分为东西北南 4 个种群，目的是为了检测地理隔离和距离隔离对新疆草兔群体遗传结构产生的影响。本研究中，从新疆草兔 4 种群的 F_{ST} 值和基因流(表 4)可以看出，F_{ST} 值都在 0.436 以上，且 $P<0.01$，可见，新疆草兔各种群之间均产生了十分显著的分化；种群间 Nm 值都小于 1，表明其基因交流非常有限。本文对新疆北部、西部、东部和南部 4 个地理种群的草兔样品的分析，共发现 44 个单倍型，各种群的单倍型多样性都很高，且各种群间并没有共享单倍型，也表明新疆草兔种群间已经发生明显的遗传分化。

Mantel tests 分析表明，新疆草兔的遗传距离与空间地理距离之间具有显著正相关性，地理距离越远，遗传距离越大。我们的研究还发现，系统树(图 3)与网络图(图 4)中，来自相同或相邻地区的草兔聚为一枝，显示新疆草兔群体存在较显著的系统地理结构。AMOVA 分析显示，新疆草兔地理群体间的变异明显大于群体内的变异(两种分析方法分别为 58.91%和 68.45%，均占 50%以上，表 3)，该结果同样说明新疆草兔存在明显的地理分化。结合 4 个地理群体的地理分布来看，天山山脉和塔克拉玛干沙漠及其广阔的距离将南部种群与其他种群分隔开来；东部种群与北、西部种群间也有沙漠和山脉的隔离，因而这些种群之间的基因交流十分困难，进而导致新疆草兔不同地理群体间显著的遗传分化。这更进一步确认了山脉和沙漠的隔离对新疆草兔群体分化有重要的影响作用。

另外，由中介网络图可以看出(图 4)，Clade A 中的单倍型主要来自西部群体和北部群体，但是有两个单倍型(H29 和 H30)却是来自东部群体。同样，Clade C 中的单倍型主要来自东部群体，但是单倍型 H33 和 H39 却是来自北部群体。这说明 4 个地理种群之间的地理隔离并不完全，它们之间还存在有限的基因流。

综上所述，新疆草兔各地理群体之间已发生明显的遗传分化，这种分化是由于地理隔离和距离隔离造成的。但是，各地理群体之间还存在有限的基因流。

3.3　亚种分化

传统意义上的亚种是指某个种的表型上相似的种群的集群，栖息在该物种分布范围内的次级地理区，而且在分类学上和该种的其他种群不同。也就是说亚种是在一定的分布区域内具有特定表型特征的同种个体的集群(Mayr & Ashlock, 1991)。传统意义上的亚种在生物多样性保护中已经被当做独立的保护单元进行保护(O’Brien & Mayr, 1991)，但是生物多样性保护更多的是为了保护遗传多样性，所以一个有效的保护单元在分子水平上也应该是一个独立的进化单元，针对这样的保护单元制定的保护策略才能真正地保护生物的遗传多样性。在对非洲野狗(*Lycaon pictus*)(Girman et al, 2001)、虎(*Panthera tigris*)(Luo et al, 2004; Luo et al, 2006)、林蛙(*Rana altaica*)(Yang et al, 2010)以及马属动物(*Equus*)(Krüger et al, 2005) 的亚种研究中，亚种在基于遗传距离构建的系统树中都以单系出现。但是也有很多传统意义上的亚种在分子水平上并没有形成一个独立进化单元(Barrowclough, 1980; Mayr & Ashlock, 1991; O’Brien & Mayr, 1991; Ball & Avise, 1992; Burbrink et al, 2000; Fischer et al, 2006)。而且，一些由形态和地理区域划分的“亚种”与分子水平上的结果并不一致，如水蛇(*Nerodia erythrogaster*)和黑马羚 (*Hippotragus niger*)(Robert et al, 2010; Alpers et al , 2004)；或被认为是不同的种，如王蛇(*Lampropeltis getula*)和壁虎(*Phelsuma*)(Pyron & Burbrink, 2009; Raxworthy et al, 2007)。本研究基于新疆草兔 mtDNA 控制区以邻接法和贝叶斯两种方法构建的分子系统树将新疆草兔分为支持率较高的 4 个独立进化枝。这 4 个进化枝与根据传统形态学定义的新疆 3 个草兔亚种并没有一一对应，其中 Clade A 主要包含来自新疆北部和西部群体样品(西域亚种)，Clade B 和 Clade C 的样品来自东部种群(中亚亚种)，Clade D 中的样品全部来自南部种群(帕米尔亚种)。在形态分类学中，新疆西部精河、温泉的草兔与北部青河、福海、富蕴、哈巴河、布尔津、阿勒泰的草兔同属于草兔西域亚种，在本文的进化树中也是聚为一枝(Clade A)。因此，我们的结果从分子角度支持传统形态分类上的草兔西域亚种的分类地位。新疆东部种群的草兔样品分聚为支持率很高的两个进化枝(Clade B 和 Clade C)，提示来自新疆东部的草兔可能存在两个亚种，而不是形态分类中的中亚亚种这一个亚种。对于形态分类中的草兔帕米尔亚种，在我们的进化树上也形成了一个独立的进化枝(Clade D)，由于其与新疆其它草兔亚种地理距离较远，生境为海拔较高地区，提示其可能达到种的分化水平。

除在系统树上形成单系外，物种内种群的分化是否已达到亚种水平还要看各进化枝之间的遗传分化是否显著(Yan et al, 2009)。我们对新疆草兔进化树上的 4 个独立枝计算了其 F_{ST} 值(表 5)，各枝系群分化十分显著(P<0.01)；图 4 显示了 Clade A～D 之间具有较多的突变步数(27～71 步)，另外，对 4 进化枝间的遗传距离的计算显示(表 5)：Clade A、B 和 C 间的遗传距离在 6.5%～7%之间，Clade D 与其他枝系群间遗传距离最大，均在 13%以上。已报道的基于 D-loop 区的中国 9 种野兔种间的遗传距离为 9.4%～16.4% (Wu et al, 2005)，雪兔和欧兔的序列差异为 12%～14.6%，雪兔群体内部的序列差异为

(0%～7.6%)(Thulin et al, 1997)。可见 Clade A、B 和 C 间的遗传分化处于亚种水平，但是 Clade D 与其他枝系间的分化可能已经达到了种间的分化水平。

来自新疆中部地区焉耆和博湖的草兔，其分类地位一直未澄清。Luo(1988)将其与东疆哈密的草兔划分为中亚亚种，而Wang(2003)则将其与新疆西北部广大地区的草兔划归为哈萨克亚种(罗泽珣称为西域亚种)，本研究包含 3 个博湖的草兔样本，划分为 3 个单倍型，其中一个单倍型与来自东疆哈密的单倍型聚为一枝；另两个与新疆西北部广大地区的草兔聚为一枝。因此，焉耆和博湖可能是中亚亚种和西域亚种的过渡地带，来自这两个亚种的样品在这个地区都有分布。

综上所述，本研究的结果支持形态分类上草兔西域亚种的分类地位，但中亚亚种被分为两个独立的进化枝，提示可能存在两个亚种；帕米尔亚种(*L.c. pamirensis*)与其他亚种间的遗传距离在 13%以上，提示其可能已达到种的分化水平。

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云南李仙江流域水电开发中的鱼类资源保护

BACK

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摘要：水电工程的开发对江河道鱼类资源产生了诸多不利影响，在保护和恢复日益增多的濒危鱼类种群的实践中，孕育和逐渐形成了保护水产学。该文对李仙江流域水电开发与流域内珍稀鱼类异鱲、越鳠、软鳍新光唇鱼和暗色唇鱼人工增殖保护实践中的实施效果和存在问题进行了分析。李仙江水电开发与鱼类增殖保护为河流鱼类的增殖保护提供了一个参考模式。但是增殖放流不是简单地一项任务，要保证整个过程得以顺利进行，需要提前进行繁育规划，提前委托，监测和增殖技术研究先行，资源保护与当地经济发展相结合。

关键词：水电开发；鱼类；增殖放流；李仙江；云南
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Fishery resource protection by artificial propagation in hydroelectric development: Lixianjiang River drainage in Yunnan as an example

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Abstract: Hydroelectric developments can result in a number of negative environmental consequences. Conservation aquaculture is a branch of science derived from conservation and population recovery studies on endangered fishes. Here we discuss the impacts on fishes caused by hydropower projects in Lixianjiang, and evaluate effects and problems on the propagation of *Parazacco spilurus, Hemibagrus pluriradiatus, Neolissochilus benasi* and *Semilabeo obscurus*. A successful propagation project includes foraging ecology in fields, pond cultivation, juvenile fish raising, prevention and curing on fish disease, genetic management, artificial releasing and population monitoring. Artificial propagation is the practicable act on genetic intercommunication, preventing population deterioration for fishes in upper and lower reaches of the dam. For long-term planning, fish stocks are not suitable for many kind of fishes, but can prevent fishes from going extinct in the wild. Basic data collection on fish ecology, parent fish hunting, prevention on fish disease are the most important factors on artificial propagation. Strengthening the genetic management of stock population for keeping a higher genetic diversity can increase the success of stock enhancement. The works on Lixianjiang provide a new model for river fish protection. To make sure the complicated project works well, project plans, commission contracts, base line monitoring and techniques on artificial reproduction must be considered early. Last, fishery conservation should be considered alongside location development.

Key words: Hydroelectric development; Fishes; Fish propagation; Lixianjiang; Yunnan

水电工程的建设对江河鱼类资源产生了诸多不利影响(Zhong & Power, 1996)。由于水电站建设规划的不同，以及河流地质、水文和水生态环境的差异，对江河鱼类资源的影响程度有所不同。为了减少水电建设对鱼类资源的影响，诞生了多种不同的鱼类保护措施。保护水产学(conservation aquaculture)是在保护和恢复日益增多的濒危鱼类种群的实践中孕育和形成的，是指利用水产学的理

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论与实践保护和恢复受到灭绝危胁的鱼类种群(Anders, 1998; Helfman, 2007)。保护水产学最核心的内容是利用保护生物学与水产学的基本理论、原理, 采用鱼类繁育计划逐步恢复濒危物种的野外种群。而迁地保育技术和人工繁殖是当前国际上保护和恢复重要鱼类种群的最主要方式之一(Helfman, 2007)。这种方法的应用在名贵的鲑、鳟等鱼类种群恢复工作中取得了十分明显的效果。在欧洲, 几乎每一条主要河流都建有土著鱼类繁殖放流基地, 其主要任务是对欧洲近 10 种特有鲑、鳟鱼类进行实施人工繁殖和放流研究工作(Helfman, 2007)。印度通过建立基因库和提供人工繁殖技术给私人养殖场, 很好地保护了濒危物种帕布绚鲶 (*Ompok pabo*)和易危物种长须鳠(*Mystus gulio*), 并恢复了它们的野外种群(Mijkherjee et al, 2002)。如果没有人工繁育计划, 美国哥伦比亚河流一带的红大马哈鱼(*Oncorhynchus nerka*)可能已经灭绝(Hebdon et al, 2004)。近年来, 在防止南美鲑形目鱼类种群数量的衰退中, 鱼类人工繁殖迅速扮演了另外一个角色, 即促进了鱼类种群的保护, 如果银大麻哈鱼(*Oncorhynchus kisutc*)没有及时制定周详的种群恢复计划, 银大麻哈鱼可能在几十年前就消失了(National Marine Fisheries Service, 2010)。

我国曾利用迁地保育和人工繁殖技术成功地提高了中华鲟(*Acipenser sinensis*)这一长江特有鱼类的种群数量(Li, 2001; Liu et al, 2007)。近年来各地科研院所纷纷开展了胭脂鱼(*Myxocyprinus asiaticus*)、齐口裂腹鱼(*Schizothorax prenanti*)、光泽黄颡鱼(*Psedobagrus nitidus*)、滇池金线鲃(*Sinocyclocheilus grahami*)等野生鱼类的人工增殖研究(Ruo et al, 2001; Wan et al, 2002; Huang & Wei, 2002; Yang et al, 2007)。这些事例说明, 迁地保育和人工繁殖技术也已成为我国土著鱼类保护和恢复技术发展的主要方向, 为大量其它土著鱼类的迁地保育和人工繁殖积累经验、提供方法。云南水电建设已在澜沧江、元江、南盘江和金沙江等流域展开(Ma, 2003)。全省水电建设中所涉及鱼类增殖保护措施的这一问题, 各水电公司都以不同的方式执行着不同程度的鱼类保护措施, 但目前尚无十分统一明确的方案规划和详细的实施规划。本文在李仙江流域珍稀濒危土著鱼类实施增殖放流保护工作取得成效的基础上, 旨在探讨鱼类人工增殖放流珍稀特有鱼类的模式, 为水电开发与鱼类物种多样性保护和管理提供一定的参考。

1　李仙江流域概况

1.1　自然概况与电站布局

李仙江流域发源于云南省大理州南涧县宝华乡石丫口山, 经把边江(龙马江)与阿墨江汇流后称李仙江, 由西北向东南, 沿江城县东北部, 经曲水乡出境流入越南。流入越南后称沱江(又称黑水河), 在越池附近汇入红河。李仙江为红河水系的一级支流, 在云南境内河道长 427 km, 天然落差 1 980 m, 流域面积 20140 km^2, 年平均流量 470 m^3/s。李仙江干流段的主要支流有绿春县大黑山镇的坝沙河和江城县曲水镇的土卡河(Department of Water Resources and Hydroelectric of Yunnan Province, 1998)。李仙江干流共有 7 座梯级电站的规划：崖羊山—石门坎—新平寨—龙马—居甫渡—戈兰滩—土卡河(图 1)。

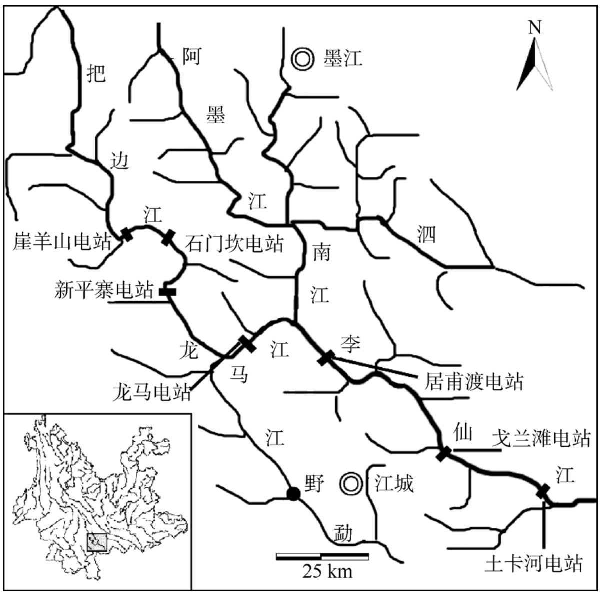

图 1　李仙江干流水电站分布

Fig. 1　Map showing the locations of hydroelectric dams in main Lixianjiang river

1.2　鱼类资源现状

通过 2003 年 5 月至 2008 年 4 月的调查, 李仙江干、支流共有鱼类 64 种(亚种), 隶属于 6 目 14 科 43 属 (Yang et al, 2010)。近年来, 李仙江鱼类资源呈现下降趋势。在电站建成之前, 渔获物主要以红鲃 (*Bagarius rutilus*)、华南鲤 (*Cyprinus rubrofuscus*) 等中大型鱼类为主；水库蓄水后，主

要渔获物个体呈小型化，急流型鱼类显著减少，湖泊型鱼类增多，华南鲤和鲇 (*Silurus asotus*) 数量显著增加，这是捕捞过度、资源衰退的表象。流域渔业主要集中在沿岸的傣族村寨，渔业收入，占部分家庭的经济总收入的30%左右。随着外来人口的增加和交通日益便捷，对李仙江流域野生鱼类的需求也急剧增长，鱼类价格大幅攀升，进一步加剧过度捕捞。

随着电鱼机数量的激增，干支流鱼类资源遭受极大的破坏。在库区实行的网箱养殖罗非鱼(*Oreochromis* spp.) 替代沿岸居民的传统农业，使得外来鱼类已在库区定居，主要外来鱼类有麦穗鱼(*Pseudorasbora parva*)、食蚊鱼 (*Gambusia affinis*)、高体鳑鲏 (*Rhodeus ocellatus*)、波氏吻鰕虎鱼(*Rhinogobius cliffordpopei*)、褐吻鰕虎鱼(*Rhinogobius brunneus*) 和莫桑比克罗非鱼 (*O. mossambica*) 等6种(Yang et al, 2010)。

1.3 渔业发展状况

建库前，李仙江流域的渔业生产仅是天然捕捞，渔获的品种复杂，且产量小，容易受季节等因素影响，难以形成规模(Yang et al, 2010)。建库蓄水后，随着库区浮游植物、浮游动物和底栖动物等的数量的增加，这为发展库区渔业提供了条件。目前，李仙江鱼类养殖业主要以水库网箱养殖为主，养殖的品种以罗非鱼养殖为主。由于养殖密度高，一些养殖户养殖的网箱鱼病滋生，造成养殖鱼类大量死亡，零散养殖，难以形成高品质的渔产品。库区养殖户对于养殖当地特有的经济鱼类热情极高，并尝试一些种类的驯养。库区养殖的罗非鱼已经发生罗非鱼链球菌病，该病是一种高感染率和高致死率的鱼病，一旦感染对象扩散至李仙江流域的土著鱼类，将对当地的本来就脆弱的渔业资源造成毁灭性的打击。

2 方 法

2.1 鱼类资源保护增殖依据

依据《云南省李仙江干流梯级水电开发环境影响报告书》、《李仙江戈兰滩水电站环境影响报告书》、《李仙江居甫渡水电站环境影响报告书》、《李仙江龙马水电站环境影响报告书》和《李仙江土卡河水电站环境影响报告书》以及云南省建设项目环境审核受理中心的云环评函 ([2006]5 号文件) 和《云南省环境保护局关于审查李仙江流域鱼类繁殖鱼苗放流和保护实施方案请示的复函》(云环函[2007]366 号)，确定软鳍新光唇 (*Neolissochilus benasi*)、暗色唇鱼 (*Semilabeo obscurus*) 和异鱲 (*Parazacco spilurus*) 为最优先保护的对象，通过对3 种鱼人工繁殖技术的攻关，最终实现每种年投放全长1.5～5.0 mm 的1～2万尾到库区适宜的河段。

根据《阿墨江普西桥水电站环境影响报告书》技术评审会会议纪要和云南省建设项目环境审核受理中心关于阿墨江水电规划环评审查意见(云环评函[2008]102 号)，确定应尽早开展鱼类增殖放流技术和增殖放流站的建设工作，确定异鱲、软鳍新光唇鱼、越鳠 (*Hemibagrus pluriradiatus*) 等3种鱼类为最优先保护的对象，最终实现每种年投放全长3.0～5.0 mm 的1～2万尾到库区适宜的河段。

2.2 鱼类增殖方案

2.2.1 增殖站的布局 参照动物迁地保护机构和设施的设计原则(Chen & Ma, 2001)，增殖站的布局需要满足迁地种群正常生存和繁衍的需要，方便管理者对迁地种群实施最大限度地保存其遗传多样性的管理，同时依然保存迁地种群野外正常生存所必需的生存技能和保存个体间正常进行繁衍的行为模式，保证迁地种群重新引入后能够适应原来的自然生存环境。

2.2.2 野生亲鱼种源收集 亲鱼采集地选择与数量确定：选择繁殖用的亲鱼的分类地位是明确的，依据动物迁地保护的理论，迁地种群维持正常生存和繁衍需要，按确定有效种群大小的50/500 法则，确定引种种群的数量，最大限度的保存和管理增殖鱼类的遗传多样性(Franklin, 1980)。

就地选择与异地选择相结合：根据进化显著单元(ESA, evolutionarily significant unit)确定种内管理单元(McClure et al, 2008)，基于可交换性定义，即根据种群在最近或历史上是否具有生态或遗传互换性来对种群进行分类，对不同种群进行分别管理(Crandall et al, 2000)；在实践中，尽可能多地收集不同的地方种群，分开饲养，科学管理，适时进行或避免种群间杂交，防止种群发生种质退化。

遗传管理与防止外来种入侵：由于迁地保育或就地保育珍稀鱼类种群通常是小种群，随机事件对小种群的影响很大；如何降低饲养种群的选择压力，圈养种群退化的方式主要包括遗传多样性的丧失、近交衰退、新的有害突变的积累和对圈养的遗传适应等方面。圈养种群的退化还表现在影响增殖放流的成功率，为了保证增殖放流成功率，就必须保持

种群遗传多样性的维持, 通过野外调查采集野生亲鱼, 及时补充人工繁殖亲鱼群体避免种群衰退。建立基因库, 通过冷冻精液和胚胎, 进行濒危鱼类物种有效保护和管理, 并做相应的 DNA 遗传多样性分析与评估。

基础生物学资料收集与积累：人工增殖对象的基础生物资料主要从历次引种考察中获得, 针对繁殖工作出现的问题, 采用专题的形式进行野外调查与室内实验。辅助采用查阅相关文献资料, 了解需要增殖鱼类的野外摄食和繁殖生态等内容(Chu & Chen, 1989, 1990; Yang et al, 2010); 同时, 通过解剖中国科学院昆明动物研究所鱼类标本库历年积累的馆藏标本, 了解鱼类的性腺发育情况、雌雄性比等内容, 以期完善鱼类繁育方案。

2.2.3　人工增殖方案　人工增殖在鱼类种群恢复计划中占有十分重要的地位。人工增殖方案包括：选择繁殖亲鱼、亲鱼的采集与繁殖、日常饲养管理、放流技术、监测与评估、捕获亲鱼计划等内容(Hard et al, 1992)。要充分认识到项目实施过程中可能遇到的主要风险, 增殖站选择是否适合亲鱼繁殖, 亲鱼寻找和收集、鱼病问题、外来种问题, 以及支持项目运作所需的经费等等; 有 1～2 套应对问题的对策或方法。

2.2.4　鱼苗流放与监测　实施鱼类人工繁育需要经常性的进行监测和评估, 监测的内容应包括评估自然种群和圈养种群遗传与生态适应之间的关系。需要每年对阶段性成果进行一次评估并根据研究进展对繁育计划进行调整。许多科学问题存在不确定性, 繁育计划就需要灵活地与项目管理相协调。

2.3 访问调查

李仙江流域的沿岸的渔民和水产站工作人员询问当地渔获物、渔业发展的情况。在访问过程中, 对当地了解需要人工增殖的鱼类生物学资料的渔民, 重点访问这些鱼类的繁殖时间、繁殖场、鱼卵性质、仔鱼出现的时间等方面的内容。

3　结　果

3.1　鱼类增殖站的建设

2008 年至 2010 年 12 月在中国科学院昆明动物研究所珍稀鱼类繁育研究基地、普洱江城基地和文山西畴基地对软鳍新光唇鱼、暗色唇鱼、异鱲和越鳠等四种鱼类的饲养和人工繁殖的实践。三地共计有大小鱼池 42 个, 20 010 余 m^2, 其中鱼类精养池 31 个, 6 670 m^2。

3.2　野生亲鱼种源收集

2008 年 4 月至 2010 年 12 月, 中国科学院昆明动物研究所在进行李仙江流域鱼类增殖项目中, 先后对云南李仙江流域、文山西畴畴阳河, 广西十万大山、北仑河等进行的 25 次鱼类引种和生态生物学调查。

目前, 圈养的软鳍新光唇鱼保存有普洱江城和文山西畴两个种群, 2 500 余尾; 暗色唇鱼保存有普洱江城和红河弥勒两个种群, 400 余尾; 异鱲保存有广西十万大山南坡和北坡两个种群, 250 余尾; 越鳠保存有红河墨江和广西北仑河两个种群, 100 余尾。

3.3　主要研发技术内容

3.3.1　摄食生态　采用野外实地调查、室内食性分析和性腺分析等方法, 详细而准确地获取各种土著鱼类(尤其是异鱲、软鳍新光唇鱼、暗色唇鱼和越鳠等 4 种鱼类)的摄食生态习性和繁殖生态习性资料。以改良的悬浮式食性分析法研究鱼类胃肠道残留食物, 快速并准确地获取鱼类食谱构成。

3.3.2　驯养繁育　确定满足这些鱼类生长和繁殖所必需的人工饲养条件。实施模拟自然环境进行驯养; 筛选合适的饲料和驯养条件。判定鱼类性腺发育的程度、产卵时间, 结合野外资料, 进一步确定这些鱼类在自然状态下繁殖所需要的水温、水流、溶氧等重要繁殖生态资料。通过准确掌握其在自然状态下的繁殖条件, 采用结合优质亲鱼培育、激素催熟、激素催情等的先进人工繁殖技术, 实施繁殖异鱲、软鳍新光唇鱼、暗色唇鱼和越鳠等珍稀特有鱼类人工繁殖技术研究。

3.3.3　苗种饲养　详细分析阿墨江天然饵料, 并广泛采集野生鱼苗鱼种, 对其食性进行分析。在此基础上, 配制适用于人工培育鱼苗鱼种的饵料, 以使鱼苗鱼种顺利度过高死亡率时期, 达到适合放流规格的鱼种。

3.3.4　鱼病防治　相对于“四大家鱼”比较, 野生鱼类在池塘驯养过程中, 由于栖息环境的变化, 诱发其对外界的反应(例如：声音、人的活动等)十分敏感; 驯化过程中的野生鱼类患细菌、真菌性和寄生虫疾病的风险增加, 常常使驯养种群遭受“灭顶之灾”。李仙江流域珍稀特有鱼类的主要疾病种类和发病规律都可能与普通的养殖鱼类不同, 需要在实际养殖过程中探索和寻找相应的治疗措施。

3.3.5　遗传管理　为了保证增殖放流成功率, 保持

种群遗传多样性的维持，通过野外调查采集野生亲鱼，及时补充人工繁殖亲鱼群体来避免种群衰退。此外，通过人工冷冻精液等方法，长期保持李仙江流域增殖的鱼类的遗传多样性。

3.3.6 人工放流 池塘的环境条件与李仙江流域各电站水库的环境存在一定差异。池塘养成的鱼苗鱼种在投放李仙江流域各电站水库前，需要进行适应性训练和试验。通过野化训练和试验，还需确定最佳的放流时间和放流地点。

3.3.7 种群监测 监测内容主要包括种群数量与遗传多样性变动两个方面，通过渔获物来调查评价各放流鱼类种群数量的变化，以及鱼类早期资源调查获得放流鱼类自然繁殖状况的有关信息，加上渔获物所获得的 DNA 材料．进行种群遗传结构与遗传多样性分析。具体研究包括分子标记的选择和筛选、自然种群的遗传多样性水平和遗传结构研究、人工增殖放流对种群遗传多样性的影响评价等方面的内容。

3.4 鱼类人工增殖实践

显然，依靠大量捕获天然亲鱼来繁殖和放流李仙江珍稀鱼类的鱼苗是不可靠和难以持久的措施。只有突破软鳍新光唇鱼、越鳠、暗色唇鱼和异鱲的人工繁殖技术，建立一定规模的人工繁育种群，大规模地生产适合放流的鱼苗，确实保护鱼类栖息地、提高鱼苗放流的存活率，才能达到有效保护软鳍新光唇鱼等物种，恢复其种群的目的。越鳠等鱼类需要的繁育条件较苛刻，其资源的保护和恢复将是一项耗资巨大和花费时间较长的一项系统工程。

3.4.1 基础资料的收集 鱼类的生活史，尤其是早期生活史比较复杂。在以往的调查往往忽视鱼类生活史的调查。许多鱼类生活史中尚未了解的关键问题，成为开展珍稀鱼类人工增殖放流的瓶颈。例如异鱲的繁殖时间、繁殖生物学、摄食生态学和早期行为生态学等资料均十分匮乏，导致人工驯化繁殖工作滞后。软鳍新光唇鱼的野外资料收集工作也是项目立项后才逐步展开的。经过数年的资料积累，目前已掌握软鳍新光唇鱼和暗色唇鱼的繁殖时间、雌雄性成熟时间、鱼卵性质、胚胎发育条件、仔稚鱼的食性及食性转化机制等方面的内容。调查前期，忽视软鳍新光唇鱼性比，加上亲鱼可供区分性别的外部特征少，很难断定适合繁殖的亲鱼性别，所以在人工繁殖实践中，可用于繁殖的雄鱼多，雌鱼少。基础资料缺乏，致使人工繁殖工作一度中断。随着水利工程建设完成后，软鳍新光唇鱼、越鳠、暗色唇鱼和异鱲的生存和繁殖条件将有较大的改变。大坝一方面加剧了阻隔作用，阻断了坝上下鱼类的基因交流。另一方面，由于改变了库区的水文格局，坝上流速减缓，以软鳍新光唇鱼为代表等鱼类原有产卵场被彻底破坏，这些因素都直接或间接影响软鳍新光唇鱼的活动，特别是自然繁殖，其自然繁殖群体可能有进一步萎缩的趋势。这一点在调查中也有所验证，也直接加剧了野外调查和引种的难度。

3.4.2 亲鱼寻找与收集 如果圈养鱼类野生群体的数量较少，又缺乏周密的繁育计划，常常会导致人工增殖对象配子质量下降，进而影响人工繁殖的催产成功率、受精率和孵化率。需要人工增殖的鱼类主要是一些珍稀濒危的种类，它们的主要特点是分布区狭小、数量稀少；因此，在收集种质资源时十分困难，很难保证圈养种群满足人工增殖任务所需亲鱼的最低数量。例如异鱲在 2003 年 5 月至 2008 年 4 月对李仙江的鱼类资源进行 8 次调查中，仅采集到一尾。而在后续引种调查中，一尾也未采集到。历史上，越鳠是李仙江下游的主要渔获对象，但水库蓄水后，捕捞引种难度增大。

3.4.3 鱼病的控制问题 相对于“四大家鱼”比较，野生鱼类在池塘驯养过程中，由于栖息环境的变化，诱发其对外界的反应(例如：声音、人的活动等)十分敏感；驯化过程中的野生鱼类患细菌、真菌性和寄生虫疾病的风险增加，常常使圈养种群遭受“灭顶之灾”。珍稀特有鱼类的主要疾病种类和发病规律都可能与普通的养殖鱼类不同，需要在实际养殖过程中探索和寻找相应的治疗措施。在人工环境下，异鱲极易感染小瓜虫病，一经感染，往往全部个体死亡，给下一步的驯化和人工繁殖等工作带来不可挽回的损失。

3.4.4 驯养与人工繁殖 通过三年的技术攻关，越鳠和异鱲等鱼类适应池塘养殖。目前已成功突破软鳍新光唇鱼和暗色唇鱼的亲鱼培育、人工繁殖和鱼苗培育等关键性技术环节，但离规模化生产还有一定距离，仍有一些关键性的技术问题尚待解决。

4 讨 论

4.1 鱼类资源保护措施比较

目前，在水电建设中对鱼类进行保护的主要措施有：建立土著鱼类资源自然保护区、重点保护鱼

类的人工增殖放流和过鱼的措施等方法。目前，运用比较多的措施主要是重点保护鱼类的人工增殖放流，而另两种措施国内鲜有研究报道。

自然保护区的建立，保护了土著鱼类赖以生存的环境，从而保存了丰富的土著鱼类物种。也可以通过工程措施对已被破坏的鱼类栖息地进行改造，完全或部分恢复原有其生态系统功能，也可以在其它区域选取宜保护物种生存环境较相似的水域(如支流)进行改造；但再造或恢复的栖息地对那些鲑、鳟等仅在祖先产卵的地方产卵的鱼类是无用的，而且费用较高，存在效果不明显的风险 (Zhu, 2005)。在过去的三十年里，欧洲和北美洲致力于恢复包括恢复鲑鱼产卵场在内的渔业健康(Brookes, 1996)，但是很多设计缺乏科学的设计，往往收效甚微(Wheaton et al, 2004a)。基于生态学、水文地貌学和工程学原理建立起来的产卵场的综合恢复方法(spawning habitat integrated rehabilitation approach, SHIRA)很好地恢复了大鳞大马哈鱼 (*Oncorhynchus tshawytscha*) 的产卵场(Wheaton et al, 2004b; Merz et al, 2006)。不管鱼类自然保护区的效果如何，但它的建立使得许多土著鱼类能在最后的庇护所里繁衍生息，同时也为人工圈养种群提供必要的野外种群补充。

鱼类人工增殖放流是使鱼类种群得以恢复的方法。由于大坝的阻隔和随之形成的水库效应，使得过去连续分布的居群被水坝分隔为多个相互隔离的小种群。部分鱼类丧失了全部或部分的生存空间。因此，开展土著珍稀濒危鱼类的人工繁殖研究，进行增殖放流是保存鱼类种质资源，保持当地土著鱼类的物种多样性有效途径之一。由于增殖放流的效果建立在对拟增殖物种生态习性具有一定研究的基础之上，增殖放流技术研究需要数年，甚至是数十年的探索，因此，增殖放流研究必须提前进行，以确保这一保护措施与大坝工程进度相协调。在鱼苗放流的环境，一般人工繁殖出苗种的繁殖成功率较自然种群低(Fleming & Gross, 1993)，而且人工增殖个体更具攻击性，与自然增殖的群体之间存在激烈的生存竞争(Buhle et al, 2009)，可能会降低野外个体的生存的几率 (Nickelson, 1986)。即使是同一进化显著单元的小种群增殖的群体可能危害原本健康的野外种群，圈养种群与野外种群相比，圈养种群繁殖出的子代具有更低的杂合性和等位基因丰富度(Blanchet et al, 2008)；大量释放其繁殖出来的鱼苗，补充野外群体，可能稀释野外群体的遗传多样性。而不是同一进化显著单元繁殖出来的个体，存在“外来种”入侵，混淆地理种群的界线。

一座完善的过鱼设施必须以拟通过设施鱼类的行为学、游泳能力、水利学和生态流量管理为设计依据(Katopodis, 2005; Novak et al, 2007)。该类方法的应用还受可供利用的资金，公众的态度及水电等部门的努力影响(Helfman, 2007)。而且，鱼道的设计非常复杂，实际使用的效果很难进行评价。过鱼效果的研究主要集中在鲑形目 (Salmoniformes), 60%以上研究主要集中在成鱼通过鱼道的效果，且大多仅集中在生活时的某一阶段(Roscoe & Hinch, 2010)。国内大多在论述如何减少水电建设对鱼类影响的措施上，提到水电项目相应建设过鱼设施，但很少涉及过鱼效果方面的讨论(Huang, 2006; Han et al, 2009)。

4.2　增殖保护对象的确立

目前，我国多数鱼类的人工增殖工作还处于比较无序状态，急需出台一部类似美国 1973 年出台的《联邦濒危动物保护法案》保护处于灭绝危险的物种，科学指导和规范列入名录的濒危动物恢复计划的实施，使实施物种恢复计划有法可依。我国目前考虑流域增殖保护对象时大多以 1989 年颁布的《中华人民共和国野生动物保护法》(Yue & Chen, 1998)、《中国濒危动物红皮书 •鱼类》(Yue & Chen, 1998)和《中国物种红色名录 •第一卷》(Wang & Xie, 2004)等所列的名录进行参考，并结合流域内具有经济、科研和开发价值的种类来确定需要增殖保护的对象，保护对象的确立，基于历史状况较多，而历史资料与现状差异大，且增殖对象的生态、生物学资料十分欠缺，对流域增殖任务的开展不具参考性；由此由此确立的增殖保护对象名录操作性差。因此，有必要在项目初期进行详尽的增殖保护对象的生态专项调查，以确立合理的增殖保护对象。

4.3　实施方案与技术措施的重要性

鱼类增殖实施方案包括硬件和软件两个部分，硬件包括能持续养殖足够亲鱼、生产足够数量苗种的鱼池和配套设施的鱼类增殖站；软件部分包括拟保护鱼类的繁殖生物学和人工繁殖技术研究及其相应的技术准备。软件和硬件两部分是相互依赖、共同配合才能真正发挥增殖保护作用。而软件部分所涵盖的鱼类繁殖生物学、人工繁殖技术及相应的技术储备是鱼类增殖保护的基础，并最终影响硬件

部分中的鱼池、水流和养殖密度设计。

多数鱼类人工繁育计划的目标是降低鱼类一个或多个生活史阶段的死亡率，尽可能多得获得鱼苗。如何长期保证圈养种群始终与自然种群是进化显著单元是人工繁育计划成功与否的关键。当自然种群数量很少时，人工繁育计划能够满足野外种群数量的增加，从而缓解濒危种群即将发生的灭绝危险(McClure et al, 2008)。圈养环境与野外环境是很不一致的，由于自然选择的作用，圈养环境所支持的遗传变量也将与野外环境所支持的很不一致(Vrijenhoek, 1998; Gustafson et al, 2007; Frankham, 2008)。以能够在野外建立一个长期自我维持的种群为标准评价了2000年以前12种主要的国际科学杂志报道的180例迁地保育案例，其中成功的案例仅有26%，而且研究结果认为这种成功率并没有提高的趋势(Fischer & Lindernmayer, 2000)。圈养繁殖大多是短期的繁育计划，仅仅一代。从长远看，圈养繁殖并不适合多数鱼类的种群恢复，但可作为防止鱼类野外种群灭绝的最后的庇护地。因此，如何建立准确的评定人工增殖鱼类的品质的体系，例如健康、遗传多样性，以提高迁地保护与放流成功的概率。放流后如何评价重新引入计划的实施效果，这些均是鱼类增殖任务所要面临的风险。因此，水电开发规划批准后及时进行流域内珍稀特有鱼类繁殖育苗放流项目的委托，委托专业单位开展研究，提前介入，保护措施的效果才有保障。

4.4 李仙江保护模式的思考

4.4.1 提前规划，提前委托 目前，鱼类人工增殖项目往往滞后于水电开发。人工增殖任务往往在水电项目完工后才开始进行规划和委托，这时河流水文条件发生了根本性改变，使得鱼类种类和数量发生了改变，增加引种难度。人工增殖需要一个较长时期的研发，如能在项目环评或项目规划一起开展，可以避免重复开展野外调查，摸清流域鱼类资源现状，为人工增殖提供科学的理论指导和技术保障。

4.4.2 增殖技术研究先行 电站建设的同时就应有相关的鱼类增殖保护措施的实施。鱼类增殖放流过程复杂，主要有亲鱼的采集、野外生态学调查、基本生物学特性研究、人工繁殖、放流技术以及放流后的监测等。这此工作都应由专门的具有专业研究人员的研究机构完成。部分水电站根据实际情况，建设有鱼类增殖站，由于缺乏专业技术人员，往往不能很好地运作。建议对新建成的增殖站进行委托管理。

4.4.3 资源保护与当地经济发展相结合 从长远展望，一个成功的增殖放流项目不仅仅能够形成成熟的技术确保物种的生存，还可以往产业化方向发展，从而带动当地经济的发展。土著特有鱼类(如软鳍新光唇鱼、越鳠、暗色唇鱼、红魾和越鳠等)的经济价值数倍于外地引入的罗非鱼等鱼类，而随着土著鱼类资源的进一步匮乏，其价值亦会进一步攀升。因此，开展土著特有鱼类人工繁殖和产业化前期生产研究，有助于促进云南省的水产养殖业从以引进种为主向以土著种为主的方向转变，品种的独特性将使产品具有不可替代性，从而获取市场竞争优势，能为养殖者带来很好的经济效益。另外，繁殖成功的土著特有鱼苗将投放到流域内的适合水域，增加鱼类存量，提高捕鱼者经济收入。

总之，李仙江水电开发与鱼类增殖保护模式，充分调动了各成员单位的工作积极性，这种模式的成功是多单位合作的结果，其成功之处主要表现在以下几方面：减少成本，节约资金，不用重复建设鱼类增殖站；团结协作，多方受益；既能进行科学研究，又能产生实际应用价值，使科学研究服务于社会；保护效果明显，可以直接增加重点保护鱼类的种群数量，可操作性强。

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滇池金线鲃亲鱼培育、繁殖力以及卵径大小与胚胎存活率的关系

BACK

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摘要：2007—2010 年，对滇池金线鲃 (*Sinocyclocheilus grahami*) 进行了亲鱼培育、繁殖力和卵径(egg diameter, ED)大小的研究。滇池金线鲃的催产率、核偏位率和孵化率分别由 2007 年的 25.2%、61.5%和 30.4% 到 2010 年的 91.3%、85.2%和 44.5%。四年间这 3 项指标均有不同程度提高，其中，催产率提高的幅度最大。提供适合滇池金线鲃营养全面的饵料可以保证亲鱼培育的最佳效果，获得高质量的鱼卵和鱼苗。滇池金线鲃绝对怀卵量与体长的关系是 $F=0.0004826SL^{3.166}$($R^2=0.6424$, $P<0.05$)。四年来滇池金线鲃的平均产卵量为(2 118.4±899.1)粒，平均绝对怀卵量为(2 402.9±881.9)粒，平均相对怀卵量为(70.4±20.8)粒。产卵量、绝对怀卵量和相对怀卵量都有随着体长增加而增加的趋势。卵的大小与胚胎存活相关，在胚胎发育的前两天，不同批次胚胎的死亡呈现一种稳定的或低的死亡率；而后 5~7 d 不同大小的卵呈现不同的死亡率，即小的卵具有更高的死亡率；而卵径>2.0 mm 的胚胎死亡率趋于稳定；大的卵有更高的生存潜力，能保证仔鱼开口前继续完善身体器官的形成或发生所需要的能量。

关键词：滇池金线鲃；亲鱼培育；繁殖力；卵径大小
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Broodstocks management, fecundity and the relationship between egg size and embryo survival ability of *Sinocyclocheilus grahami*

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Abstract: Broodstock management, fecundity and egg size of the golden-line barbel *Sinocyclocheilus grahami* were studied from 2007 to 2010. The induced spawning success of female *S. grahami* was 25.2% in 2007 and dramatically increased to 91.3% in 2010. The nucleus deviation rate and hatching success were 61.5% and 30.4%, respectively, in 2007 and increased to 85.2% and 44.5%, respectively, in 2010. Providing nutritious food for broodstocks of *S. grahami* can ensure optimum breeding conditions as well as high-quality eggs and fingerlings. There also seems to be a relationship between absolute fecundity (F) and standard length (SL), as described by the power-exponent function $F=0.0004826SL^{3.166}$ ($R^2=0.6424$，$P<0.05$). The average of number of spawn egg was 2118.4±899.1 from 2007 to 2010, the average of absolute fecundity was 2402.9±881.9 from 2007 to 2010, and the average of relative fecundity was 70.4 ±20.8 from 2007 to 2010. The number of spawn egg, absolute fecundity and relative fecundity increased in individuals with a longer body length. Additionally, egg size contributed to the survival rate of embryos. The different batches reached an asymptotic, low or stable embryonic mortality during the first two days; the balance was broken in the subsequent seven days, as high embryonic mortality was observed in smaller eggs. The mortality of embryos from eggs larger than 2.0 mm was, contrastingly, rather stable. Embryos from bigger eggs have stronger survival potential, as bigger eggs can provide more energy and thus, a more favorable environment for early development.

Key words: *Sinocyclocheilus grahami*; Broodstocks management; Fecundity; Egg size

社会日益增长的物质生活需求和拯救珍稀物种的环保要求都迫切要求对野生特有珍稀鱼类进

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行驯养和人工繁殖的研究。但是, 大多数野生鱼类从野生环境迁移到人工池塘饲养时, 往往不能实现自我繁衍。在人工控制的环境条件下注射人工合成激素, 是实现野生鱼类的自我繁殖或人工助产的有效途径之一(Slater et al, 1995; Brzuska, 2003; Yang et al, 2007; Gullu et al, 2008; Pan et al, 2009a)。鱼卵质量被定义为鱼卵具有被受精并完成随后胚胎发育的能力(Brooks et al, 1997; Bonnet et al, 2007)。了解引起鱼卵质量变化的因素, 并有针对性调控这些因素以达到提高鱼卵质量, 是实现人工繁殖的关键。通常认为鱼卵质量与外部环境和繁殖条件密切相关, 即鱼卵的质量受人工诱导亲鱼成熟的方法、环境和营养条件等因素影响(Cadrin et al, 2005)。亲鱼培育方案直接关系到性腺成熟度、催产率、鱼卵的受精率和孵化率, 完善的培育方案能显著提高鱼卵与仔鱼的质量 (Izquierdo et al, 2001)。在生产实践中, 通常认为在亲鱼繁殖之前的几个月开始投喂高质量的饲料可以显著地改善其繁殖性能(Izquierdo et al, 2001)。繁殖力(fecundity)是衡量鱼类繁殖性能的主要指标之一, 而繁殖力常常使用怀卵量和产卵量作为评价指标(Yin, 1995)。卵径大小(egg size)对鱼的早期发育和存活具有重要的生物学意义, 是评价鱼卵质量最常用的参数之一(Yin, 1995)。无论是满足商业生产还是增殖放流对鱼苗的需要, 一个完善的亲鱼培育方案, 对于获得大量高质量的鱼卵和鱼苗显得尤为重要, 是其实现规模化生产和有效物种进行迁地保育、恢复野外种群的前提条件。

截至目前, 金线鲃属（*Sinocyclocheilus*）鱼类记载有 55 种, 广泛分布在云贵高原及广西壮族自治区(Zhao & Zhang, 2006)。以往有关金线鲃属鱼类的研究多集中在新种描述和系统发育研究(Chu & Cui, 1985; Wang et al, 1999), 而生态生物学的研究较少(Zhao & Zhang, 2009)。目前, 仅见于滇池金线鲃（*Sinocyclocheilus grahami*）、抚仙金线鲃(*Sinocyclocheilus tingi*)和尖头金线鲃(*Sinocyclocheilus oxycephalus*)的繁殖研究报道, 内容涉及亲鱼培育、人工繁殖、仔稚鱼食性转化和生长(Yang et al, 2007; Pan et al, 2009a, b; Yan et al, 2009)。历史上, 滇池金线鲃(*Sinocyclocheilus grahami*)是滇池沿岸渔民的主要渔获对象。酷渔滥捕、围湖造田、水质污染和盲目引种都是滇池金线鲃生存所面临的威胁因素(Chen et al, 1998; Pan et al, 2009c; Zhao & Zhang, 2009)。该物种于 1989 年被列为国家 II 级保护动物, 在《中国濒危动物红皮书・鱼类》中被列为濒危等级(Yue & Chen, 1998)。本文旨在通过对滇池金线鲃亲鱼培育、繁殖力和鱼卵质量的研究, 探讨在不同培育方式下亲鱼的繁殖潜力, 以期优化滇池金线鲃亲鱼培育方案, 提高滇池金线鲃鱼卵和仔鱼品质。

1　材料与方法

1.1　亲本来源与饲养方案

亲本系 2005 年 5—7 月采集自昆明嵩明牧羊河, 饲养在中国科学院昆明动物研究所珍稀鱼类保育研究基地(海拔：2 008 m; N：25°02′37.2″, E：102°55′24.3″)。2006 年之前, 亲本从野外引种到基地后, 主要进行适应性驯化饲养, 解决亲鱼的饵料和日常管理等问题, 亲鱼的培育在 2006 年 1 月—2010 年 4 月间进行, 具体的亲鱼培育过程如下：

2007 年度的亲鱼培育措施：2006 年 1 月—2007 年 4 月, 将滇池金线鲃亲鱼饲养在 300 m^2、水深为 1.5 m 的泥底池塘中, 全年投喂 111 鲤鱼种鱼饲料(颗粒直径=2.0 mm, 通威股份有限公司昆明分公司)。采用自然水温, 全年水温范围为 7～28 ℃, 水温过高和过低时, 采用注水降低或升高水温。2007 年 3 月进行人工繁殖试验。

2008 年度的亲鱼培育措施：2007 年 5 月—2008 年 1 月, 亲鱼的培育方案同上一年度; 2008 年 2 月—4 月将鱼转入在面积为 50 m^2、水深为 1.2 m 的水泥池中, 饲养期间以投喂 111 鲤鱼种鱼饲料为主, 并混合部分粗蛋白含量 40%的粉状饲料, 并逐渐增大粉状饲料的投喂量。

2009 年度的亲鱼培育措施：2008 年 5 月—10 月 31 日, 亲鱼饲养在面积为 50 m^2、水深为 1.2 m 的水泥池中, 饲养期间投喂 111 鲤鱼种鱼饲料; 2008 年 11 月 1 日以后陆续将亲鱼放入 2.0 m×1.0 m×1.2 m 玻璃水族缸中强化饲养, 投喂粗蛋白含量 40%的粉状饲料为主, 并混合部分活饵。水族缸水位保持在 0.8 m, 水的过滤速度为 18 L/min, 实时溶氧量>6 mg/L, 在整个试验过程中, 水温控制在 16～21℃。在进行人工繁殖时, 亲鱼至少在水族缸中饲养 30 d。

2010 年度的亲鱼培育措施：2009 年 5 月—2010 年 3 月, 全年保证亲鱼各个时期的营养, 全年饲养在玻璃缸内, 饵料主要以 111 鲤鱼种鱼饲料和蛋白含量为 40%的粉状饲料为主, 辅以活饵、改善繁殖

的矿物质和维生素等。水温控制在16～21℃，并营造流水环境。

1.2 亲鱼的日常管理

1.2.1 亲鱼的选择标准 选作繁殖用的雌鱼，一般为3龄以上、体重30 g以上；雄鱼2龄以上、体重20 g以上。具体要求为体色鲜艳、体质健壮、活动能力强、鳞片和鳍条完整，在饲养期间没有发生过鱼病。在选育过程中，为防止种质退化，及时淘汰自然突变产生的不良个体。

1.2.2 雌雄鉴别 在非繁殖季节，滇池金线鲃雌雄第二性征不明显。在繁殖季节，滇池金线鲃雌雄可供区分的第二性征不多。主要的区别特征为：雌鱼腹部外观饱满、膨大而柔软，泄殖腔较大、红肿突出；雄鱼腹部狭长略硬，泄殖腔较小、略向内凹不红肿。

1.2.3 培育池与亲鱼放养 滇池金线鲃属于小型鱼类，培育池面积不宜过大，养殖池塘以50~200 m^3、水深以1.0~1.5 m为宜，具体要求背风向阳、排灌方便。便于排水，捕捞亲鱼进行检查。滇池金线鲃养殖密度通常要低($<3\mathrm{kgm}^{-3}$)，雌雄比1∶1.5。放养前用高锰酸钾全池泼洒消毒，然后注入新水，用遮光率90%的黑色遮光网遮盖，避免阳光直射。池内每5 m^{2}布置一个砂头充气，增加池内溶氧。

1.3 人工繁殖与孵化

参照滇池金线鲃人工繁殖方法(Yang et al, 2007)，催产素采用马来酸地欧酮(DOM，宁波第二激素厂)和促黄体素释放激素A$_2$(LHRH-a$_2$，宁波第二激素厂)。剂量按每公斤体重1 mg马来酸地欧酮+ 1 μg促黄体素释放激素A$_2$，雄鱼注射量减半，用0.9%的生理盐水稀释混合后，肌肉注射。注射后24 h左右施行人工助产、干法受精。

在进行人工繁殖之前，测量每条雌鱼产卵前的体重(spawn before body weight, W)、产卵后的体重(spawn after body weight, W$_a$)、体长(standard length, SL)、全长(total length, TL)和挤出的未受精时的卵重(egg weight, EW)；计数每条雌鱼产出的鱼卵数量，具体方法为取出0.2 g左右未受精的卵子进行计数，并测量卵膜未膨大时的卵径(egg diameter, ED)。完成人工授精操作后，鱼卵及时用霉菌净(重庆富尔家动物药业有限公司)消毒15 min，从每尾雌鱼采集到鱼卵中取出50粒放在塑料盆中孵化，并在蔡司解剖镜(Zeiss Stemi 2000-C, Germany)下，计数其受精和胚胎发育各阶段的死亡数，胚胎发育时相及名称依据Ma et al(2008)。

1.4 数据收集

怀卵量(fecundity)是指成熟雌鱼的怀卵粒数，一般又称绝对怀卵量(absolute fecundity, *F*)；相对怀卵量(relative fecundity, *RF*)是指雌鱼单位体重产出的卵粒数，即$RF = F/W_a$，式中F是绝对繁殖力，W_a是产卵后雌鱼的体重。产卵量(number of spawned eggs, *PE*)是指通过人工繁殖挤出雌鱼的鱼卵粒数。催产率(induced spawning success, *IS*)是指产卵雌鱼数，占催产雌鱼数的百分比，即$IS=(N_h/N_t)\times100$，式中N_h为产卵的雌鱼数量，N_t为全部催产雌鱼的数量；产出率(spawning success, *S*)是用来评价每个雌鱼的催产效果，即$S=(PE/f)\times100$，式中f是根据全长-绝对怀卵量相关公式所推算的怀卵量。肥满度(condition factor, CF)：$CF=W/\hat{W}$，式中W是实测体重，$\hat{W}$为按长重相关公式推算的体重(Yin, 1995; Kreiner et al, 2001)；核偏位率(nucleus deviation rate, *ND*)是指从每尾雌鱼所产出的鱼卵中随机抽取20粒，放置于10%的醋酸溶液中，根据观察核偏离情况确定鱼卵潜在的受精率，即$ND =(N/20)\times100$，式中N表示发生核偏离的鱼卵粒数。胚胎存活率(rate of embryonic survival)是指胚胎发育到某一发育时相时存活的胚胎数量与所观察胚胎数量总数的比值。孵化率(hatching success)是出膜的仔鱼数量与总受精鱼卵数的比值。生存率(survival success)是指仔鱼出膜时的存活率，即出膜的仔鱼数量与所有产出鱼卵数量的比值(Yin, 1995)。产后死亡率(death after hatching, *SDH*)是指在一个繁殖季节死亡的亲鱼的数量与全部参加催产繁殖的数量的比值。

1.5 数据处理

各测量数据均采用平均数±标准误(mean±*SD*)。用单因素方差分析和回归分析比较分析处理数据，所有数据处理和制图均在Sigmaplot 2001和Statgraphic中进行。显著性水平为$P<0.05$。

2 结果

2.1 亲鱼的培育

滇池金线鲃是杂食性鱼类，偏爱动物性饵料。饲养滇池金线鲃亲鱼时常用的饲料为的111鲤鱼种鱼饲料(颗粒直径=2.0 mm，通威股份有限公司昆明分公司)。饵料的日投喂量为亲鱼体重的3%左右，且应该视天气、水温和鱼的摄食情况灵活掌握，每次的投喂量以0.5~1 h吃完为度。一般一天投喂两

次，上午和下午各一次。

滇池金线鲃以 IV 期卵巢越冬，所以亲鱼的培育重点应该在夏、秋两季。冬天的投喂量以能维持正常生长即可。但是，滇池金线鲃常年生活的水温较低环境中，在冬季仍能大量觅食食物，因此，在天气晴好、水温较高时，需酌情增加投喂量。在产前 1~2 个月，应对亲鱼进行强化培育，可以适当增加饵料中粗蛋白的含量，以加速滇池金线鲃性腺成熟。在此期间以投喂颗粒饵料为主，适当投喂水蚯蚓、昆虫等动物性饵料，有助于亲鱼性腺发育。临近产卵，亲鱼的摄食量明显减少，表明滇池金线鲃亲鱼性腺发育成熟良好，此时可以停止投喂，以防止造成因饱食判断成熟度不准确。

在整个亲鱼培育期间，冲水次数与频次依季节、水质肥瘦和鱼的摄食情况灵活掌握。通过加注新水，可以改善水质。在秋末和冬季水温低时，注水次数减少，每 5~7 d 冲水 1 次，每次 1 h 左右；春季气温开始转暖时，每隔 3~5 d 注水 1 次，每次 1~2 h；产前 1~2 个月可以适当增加冲水次数。前期一般 2~3 d 冲水 1 次，后期 1~2 d 冲水 1 次，每次冲水 2~3 h；在催产前几天最好每天都冲水或给以微流水刺激，以促进亲鱼性腺的进一步发育成熟。

2.2　繁殖力与卵径大小

根据 25 尾 IV～V 期性腺样品 1 056 粒沉积卵黄的卵粒统计分析，滇池金线鲃怀卵量与体长存在的关系是 $F=0.0004826SL^{3.166}$($R^2=0.6424$，$P<0.05$)。四年来滇池金线鲃的平均产卵量为(2 118.4±899.1)粒，平均怀卵量为(2402.9±881.9)粒，平均相对怀卵量为(70.4±20.8)粒。怀卵量、产卵量和相对怀卵量都有随着体长的增加而增加的趋势，三者与体长的关系可用下列方程表示：

$$F = 0.0006614SL^{3.102}$$

$$PE = 0.1267SL^{1.997}$$

$$RF = 100.8-0.2368SL$$

2007—2010 年间每年滇池金线鲃体长与产卵量、相对怀卵量的关系，根据实测数据，各年度的平均产卵量与相对怀卵量如表 1 所示，同时它们之间的关系，如图 1、2 所示。个体产卵量波动于 1 500～4500 粒之间，平均为 2400 余粒。它与体长的关系是一个曲线增长关系。从表 1 和图 1、2 均可看出滇池金线鲃产卵量和相对怀卵量都随体长的增长而有规律性的增大。

通过历年的努力，滇池金线鲃在产卵量、相对怀卵量、卵巢体积和卵径等方面有逐年提高的趋势。在繁殖季节，通过控制一些外部因子，如亲鱼饵料、繁殖的操作方法和水质等能提高鱼卵的质量，进而提高鱼苗质量。

根据观察，胚胎从受精发育到原肠胚晚期大概需要 48 h，在这段时间内胚胎的死亡率均较低，每个阶段死亡为 5%~10%之间(表 2)，不同卵大小胚胎的死亡呈现一种稳定的或低的死亡率，即胚胎在完成原肠胚之前各胚胎发育时相的胚胎死亡率都较低；进入体节期后，因为卵子质量不佳而造成的孵化过程中的大量死胚。因为处于轻度过成熟的卵子，即使精子进入卵内，也能暂时出现卵裂，但到原肠胚以后就会陆续出现畸形或中途死亡；在孵化的

表 1　2007—2010 年滇池金线鲃雌鱼的人工繁殖效果

Tab. 1　Results from artificial propagation of female *Sinocyclocheilus grahami* from 2007 to 2010

项目 Items	Mean ± *SD* (50♀/Year)			
	2007	2008	2009	2010
产出率 Spawning success (%)	$1819.6±695.2^{a3}$	$1978.9±755.2^{ab}$	$2180.1±853.8^{bc}$	$2495.1±1113.8^{c}$
相对怀卵量 Relative fecundity (%)	$79.7±25.0^{a}$	$62.8±12.2^{b}$	$69.3±21.1^{bc}$	$69.6±19.8^{c}$
卵巢体积 Ovary volume (mm³)	$5509.3±3048.5^{a}$	$7177.9±3891.5^{b}$	$8300.9±4025.8^{b}$	$10587.2±6038.0^{c}$
卵径 Egg size (mm)	$1.76± 0.17^{a}$	$1.87± 0.13^{b}$	$1.92± 0.11^{b}$	$1.97±0.13^{c}$
相对怀卵量 Relative fecundity (%)	$90.8±27.4^{a}$	$88.8±18.6^{a}$	$91.8±28.4^{a}$	$87.6±23.6^{a}$
催产率 Induced spawning success (%)	25.2	74.8	90.3	91.3
核偏位率 Nucleus deviation rate (%)	$61.5±25.9^{a}$	$86.6±11.6^{b}$	$80.6±18.6^{b}$	$85.2±17.9^{b}$
孵化率 Hatching success (%)	$34.9±22.1^{a}$	$36.1±20.8^{a}$	$30.4±21.4^{a}$	$44.5±17.5^{b}$
生存率 Surviving success(%)	$27.0±22.9^{a}$	$33.5±21.2^{a}$	$26.9±21.4^{a}$	$41.0±18.2^{b}$

同一行数值上标不同字母表示有显著差异 $P<0.05$；相同字母表示无显著差异。

Values in the same row with different superscripts denote significant differences at $P<0.05$, same superscripts denote no significant difference.

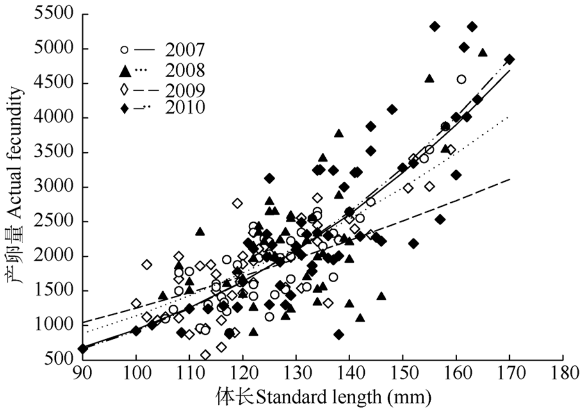

图 1 2007—2010 年滇池金线鲃产卵量与体长关系

Fig. 1 Relationship between number of spawned eggs and standard length of female *Sinocyclocheilus grahami* from 2007 to 2010

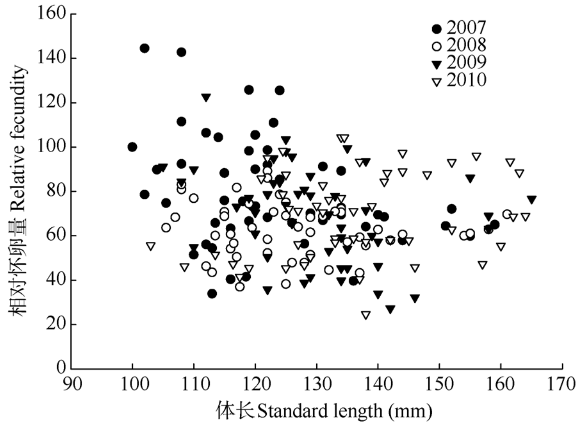

图 2 2007—2010 年滇池金线鲃相对怀卵量与体长关系

Fig. 2 Relationship between relative fecundity and standard length of *Sinocyclocheilus grahami* from 2007 to 2010

3~7 d 里不同大小的卵呈现不同的死亡率，即小的卵有更高的死亡率；而卵径达到 2.0 mm 以上胚胎死亡率趋于稳定，并保持较高的生存率，但各组的孵化率差异则较小(表 2)。

2.3 催产率、核偏位率和孵化率

由于技术的改进，在 4 年里催产率的提高最为明显，催产率由 2007 年的 25.2%提高到目前的 90%左右。除 2007 年对人工受精技术掌握的不够全面外，其它 3 年的鱼卵的核偏位率始终保持在 80%以上，在选择鱼卵最佳受精时间上有大幅度的提高；随着卵径的增加，相应的雌鱼卵巢的体积也随之增加(表 1，图 3)。而孵化率和生存率的提高比较缓慢，这主要与池塘驯养的鱼类出现生殖功能紊乱主要由于捕获诱发的压力和缺乏合适的繁殖条件引起的。

表 2 滇池金线鲃不同卵径大小的胚胎存活率和孵化结果

Tab. 2 Differences in embryonic survival and hatching due to egg size of *Sinocyclocheilus grahami*

	平均卵径 Average of egg size (mm)			
	≤1.6	(1.6, 1.8]	(1.8, 2.0]	>2.0
观察批次 Number of batches observed	11	46	95	48
核偏位率 Nucleus deviation rate (%)	27.0	56.6	87.5	93.3
胚胎存活率 Rate of embryonic survival (%)				
囊胚期 Blastula period	90.1	92.5	91.3	94.9
原肠胚早期 Early gastrula period	85.3	86.7	89.7	90.4
原肠胚晚期 Late gastrula period	45.2	47.4	73.4	85.7
体节早期 Early segmentation period	40.9	42.1	68.2	73.6
孵化期 Hatching period	13.6	22.4	48.8	55.9
孵化率 Hatching success (%)	29.3	37.4	43.7	54.1
生存率 Survival success (%)	11.1	19.4	40.2	52.4

2.4 亲鱼护理

在进行滇池金线鲃人工繁殖的四年中，产后雌雄亲鱼的死亡率均低于 0.5%，雌鱼每一个繁殖季节的死亡率变化不大，而雄鱼的死亡率则逐年下降，2010 年雄鱼的死亡率仅 0.152%(表 3)。在每年死亡的亲鱼中，多数为人工繁殖操作和亲鱼难产造成，

表 3 2007—2010 年人工繁殖用滇池金线鲃的体长、体重和肥满度

Tab. 3 Standard length, body weight and condition factor of *Sinocyclocheilus grahami* for artificial propagation from 2007 to 2010

项目 Items	2007		2008		2009		2010	
	♀	♂	♀	♂	♀	♂	♀	♂
测量数量 NR^1	50	50	50	50	50	50	50	50
体重(g) W	24.0±10.3	16.1±3.2	31.7±11.0	18.7±8.1	32.3±9.8	23.4±11.5	35.5±11.1	30.3±13.2
体长(mm) SL	122.7±14.2	101.2±3.5	126.3±13.2	109.5±9.7	130.0±12.6	118.8±10.9	135.8±14.4	125.2±12.7
体重-体长关系 $W=aSL^b$	$W=0.018SL^{2.83}$	$W=0.017SL^{2.74}$	$W=0.011SL^{3.02}$	$W=0.014SL^{2.93}$	$W=0.015SL^{2.98}$	$W=0.012SL^{2.77}$	$W=0.024SL^{2.79}$	$W=0.022SL^{2.65}$
肥满度 CF	1.006±0.10	1.010±0.02	0.999±0.03	1.032±0.07	1.004±0.06	0.9754±0.04	1.007±0.11	0.9856±0.02
繁殖总量 NT	1127	2589	1984	3502	2449	3081	2512	3301
产后死亡率(%) SDH	0.354	0.386	0.454	0.400	0.449	0.227	0.477	0.152

NR^1 = Number of fish researched; NT = Number of total broodstocks in each years.

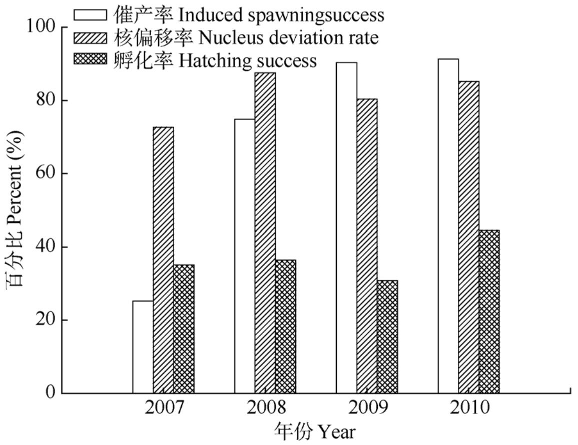

图 3　2007—2010 年滇池金线鲃的催产率、核偏位率和孵化率

Fig. 3　Induced spawning success, nucleus deviation rate and hatching success of *Sinocyclocheilus grahami* from 2007 to 2010

占全部死亡的 80%左右; 同时, 在繁殖过程中, 亲鱼因发情、产卵等生殖活动, 体力消耗很大, 对疾病的抵抗能力变弱, 加上进行人工繁殖的多重操作, 往往会引起亲鱼腹部或体侧充血, 皮肤损伤, 体表创伤, 稍有管理不善, 极易继发肤霉病。因此, 应对产后的亲鱼应精心护理。在四年的人工繁殖中, 对亲鱼进行护理的基本要点是：拉网时细心操作; 亲鱼入池后, 精心饲养, 为下一年度的人工繁殖提供优良的亲鱼做准备。

3　讨　论

3.1　亲鱼培育技术及其效果

亲鱼培育技术的形成主要通过了解需要培育亲鱼性腺发育特点、繁殖习性和影响产卵繁殖的生态环境因素。在生产实践中逐步掌握该种鱼类日常生活习性和性成熟对水溶解氧、温度、pH 值、水流速度等的基本要求, 探讨如何通过人工途径满足其基本物理化学环境的途径和方法, 达到实现其人工繁殖成功, 并获得大量高质量鱼卵和仔鱼。四年的人工繁殖实践显示：一套亲鱼培育方案并不能满足所有饲养的种群。但随着滇池金线鲃自然种群逐渐适应池塘养殖环境和亲鱼培育方案的完善, 也越来越容易获得高质量的鱼卵和精子。鱼类人工繁殖技术在传统渔业上, 为水产养殖提供了大量养殖的鱼苗。但随着鱼类种群数量的衰退, 近年来, 在防止南美鲑形目鱼类种群数量的衰退中, 鱼类人工繁殖迅速扮演了另外一个角色, 即促进了鱼类种群的保护, 如果银大麻哈鱼(*Oncorhynchus kisutch*)没有及时制定周详的种群恢复计划(包括鱼类繁育计划), 银大麻哈鱼可能在几十年前就消失了(National Marine Fisheries Service, 2010)。

亲鱼培育技术可以通过繁殖中所获得鱼卵质量的好坏的加以改进与完善, 而鱼卵质量的提高有赖于培育出高质量的亲鱼。但是在人工养殖实践中, 判定和评价鱼卵质量十分困难, 这主要是在孵化鱼卵过程中很难模拟出鱼卵最佳的孵化条件。狼鲈(*Dicentrarchus labrax*)和金头鲷(*Sparus auratus*)的孵化率一般只有 5%~15%, 大西洋庸鲽(*Hippoglossus hippoglossus*)的孵化率更低, 仅仅 1%的孵化率(Brooks et al, 1997)。但是如果孵化率超过 50%, 鱼卵质量评价体系则可以建立, 卵子和精子质量评价体系的建立有助于改进和完善亲鱼培育方案。

3.2　亲鱼培育与催产效果的关系

一些具有重要经济价值的鱼类, 试图通过人工环境下, 扩大其繁殖规模, 但往往很难达到此目的。这主要是由于在人工饲养环境下鱼类的生殖功能紊乱引起的, 而且往往表现在雌鱼方面(Gui et al, 2007); 亲鱼培育的首要任务是尽可能减少捕获所诱发的压力和加强培育过程中亲鱼的营养需求, 以期获得最好的繁殖效果(Cabrita et al, 2009)。通过统计催产率可以评价亲鱼培育和催产技术的效果, 并能为下一繁殖季的亲鱼培育提供改进依据。滇池金线鲃亲鱼催产效果分为 3 种：全产(个体催产率：80%～100%)、半产(20%～80%)和不产(0%～20%)。雌亲鱼在激素的作用下, 控制好水温, 基本能在预定的时间内通过人工挤卵的方式将成熟的卵子全部排空, 其特征是雌鱼腹部明显空瘪, 腹腔内没有或仅有极少数卵子残存。催产效果为半产的个体主要是由于雌鱼的体质较差、受伤较重等因素引起的; 可能也与催产激素注射后的水温偏低和外界惊动干扰所致, 导致雌鱼成熟度较差, 导致卵巢内的卵子发育不整齐。半产的卵子通常受精率和出膜率均较低。亲鱼不产主要原因是亲鱼成熟度很差或已经退化, 也可能是亲鱼培育期间发生比较严重的鱼病, 造成亲鱼培育不够。雌鱼腹部异常膨大, 轻挤腹部时, 挤不出卵, 只有混浊略带黄色的液体或血水流出。主要是因为卵巢过熟并且已经退化, 注射的激素剂量过大也能导致卵的成熟和排卵失调, 或可能是由于雌亲鱼体质差, 鱼体受伤或生殖孔被卵块堵塞, 亲鱼难产或滞产引起的。

因此, 在亲鱼培育管理中要最大限度地降低捕

获诱发的压力, 尽量提供适合的养殖条件, 如池塘的大小、水质和光强度等, 但是对于许多鱼类而言, 要完全模仿鱼类繁殖季节的生态环境几乎是不可能。确保滇池金线鲃在繁殖季节成功繁殖, 首要考虑的因素是亲鱼培育阶段的营养, 其次是池塘环境、水质、空间和温度等。

3.3 卵径大小与胚胎存活

在胚胎发育过程中, 胚胎的死亡原因是多样的, 但在胚胎发育的前两天, 不同批次胚胎的死亡呈现一种稳定的或低的死亡率; 而后的 7 d 里不同大小的卵呈现不同的死亡率, 卵径达到 2.0 mm 以上的胚胎死亡率趋于稳定, 而大小不均一、平均卵径小于 2.0 mm 的鱼卵的死亡率较高。这表明，各个阶段胚胎的存活率与卵径大小有关, 一般卵大的胚胎更容易存活, 但是由于在孵化过程中胚胎发育的各个阶段对温度、溶氧和 pH 的敏感度不同, 也可能导致胚胎畸形或死亡。这说明雌鱼性腺发育程度不好, 其真实的受精率很低, 并可能导致生存率低。前两组(<1.8)在原肠期的大量“死亡”的卵很可能是未受精的, 后两组因受精率较高因而没有原肠胚死亡率较高的阶段。

通常认为, 大卵径的鱼卵质量优于小卵径的鱼卵, 但是雌鱼产出鱼卵的大小受食物时空变化、性成熟年龄、捕食和自身体长等的影响(Brooks et al, 1997), 因此, 亲鱼培育的效果好坏直接反映在鱼卵质量上, 可以从外观上鉴别鱼卵质量的优劣。质量较高的鱼卵呈橙黄色, 大小比较均匀、饱满, 且弹性强。受精率比较高, 吸水后迅速膨胀。在胚胎发育过程中, 所有胚胎的时相比较均一, 时序正常。不熟或过熟的卵子颜色较淡, 大小不均匀, 受精率低, 不圆, 弹性差, 吸水膨胀较慢或吸水差, 卵裂不整齐, 通常在神经胚之前胚胎大量裂解。

在滇池金线鲃人工繁殖的生产实践中, 对每尾雌性亲鱼的卵子直径测量时发现, 部分亲鱼的鱼卵里掺杂着少数“白卵”。据测量结果, “白卵”卵径, 一般为小于 1.8 mm, 属于不成熟卵子。这部分卵子主要是随着人工繁殖过程中, 挤压鱼的腹部随着成熟的卵子流出体外。抚仙金线鲃的人工繁殖也有类似的情况, 其受精率达到 80%, 但是孵化率较低(Pan et al, 2009a)。

3.4 亲鱼产后低死亡率的意义

滇池金线鲃属于国家 II 级的保护动物, 其野外种质资源十分稀少和珍贵, 进行野外引种和驯养繁殖需要办理《中华人民共和国水生野生动物驯养繁殖许可证》和《中华人民共和国水生野生动物经营利用许可证》。如果亲鱼产后的死亡率过高, 不可避免地需要每年从野外进行引种, 这无疑会对本来就十分濒危的野外种群造成不小的压力。再加上对圈养种群的遗传多样性缺乏有效的管理、盲目放流, 势必不利于滇池金线鲃的长期保育工作的开展。四年来始终将产后亲鱼的死亡率控制在 0.5%以内, 不仅避免重复引种, 辅之对圈养种群不同地方种群的遗传多样性管理和科学的进行增殖放流, 是有效保护滇池金线鲃的途径之一。

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中国鲃亚科金线鲃属鱼类一新种——黄田金线鲃 (鲤形目：鲤科)

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摘要：该文记述了采自广西贺州市贺江水系——洞穴的鲤科鲃亚科金线鲃属鱼类一新种，命名为黄田金线鲃(*Sinocyclocheilus huangtianensis* Zhu, Zhu *et* Lan sp. nov.)。新种眼睛正常，背鳍末根不分枝鳍条柔软，后缘无锯齿，与属内同分布在贺江水系的已知种季氏金线鲃及邻近漓江水系的桂林金线鲃相似，但新种侧线鳞为 52～59 枚，侧线上鳞 17～23，侧线下鳞 16～17，围尾柄鳞 40～46，鳃耙 9～10，眼径为体长的 4.3%～5.4%，眼间距为体长的 9.2%～9.6%，口宽为体长的 6.0%～7.3%，与季氏金线鲃和桂林金线鲃有明显区别。

关键词：鲤科；金线鲃属；新种；洞穴鱼类；中国
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Description of a new species of Barbinae, *Sinocyclocheilus huangtianensis* from China (Teleostei: Cypinidae)

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Abstract: A new species, *Sinocyclocheilus huangtianensis*, is found from a cave of Hejiang River, Hezhou, Guangxi, China. This river is a tributary of the Pearl River. It is similar to *S. jii,* distributed in Hejiang and *S. guilinensis* distributed in Lijiang by having a soft dorsal spine without serration and normal eyes. The combination of the following characteristics makes this new species different to *S. jii* and *S. guilinensis*: (1) the lateral line scales 52–59, up lateral line scales 17–23, the down lateral line cales 16–17, the circumpeduncular scales 40–46; (2) gill raker 9–10; (3) eye diameter/SL 4.3–5.4%; (4) interorbital width /SL 9.2–9.6%; and (5) mouth width/SL 6.0–7.3%.

Key words: Cyprinidae; *Sinocyclocheilus*; New species; Hpogean fish; China

金线鲃属(*Sinocyclocheilus*)隶属于鲤科(Cyprinidea)鲃亚科(Barbinae)，是我国特有属，属内所有物种都有不同程度的洞穴生活习性。因洞穴的隔离作用，属内的物种多样性非常丰富，目前有 49 个有效种(Zhao & Zhang, 2009)，但仅分布在云南东部、贵州的中南部和广西的西北部、北部。作者于 2010 年 6 月在广西壮族自治区贺州市一洞穴中采集到一批金线鲃属鱼类标本，经鉴定认为是一新种，特加以报道。

1 材料与方法

研究标本均经 10%福尔马林固定后保存。测量方法主要参照 Zhao & Zhang(2009)。测量使用游标卡尺，精确记录至 0.1 mm。季氏金线鲃和桂林金线鲃形态特点描述和数据参照 Zhao & Zhang(2009)及 Zhang & Dai(1992)。

2 新种描述

黄田金线鲃，新种 (*Sinocyclocheilus huangtianensis*

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Zhu, Zhu et Lan sp. nov.)

正模标本：2010003，体长 115.0 mm(图 1), 2010 年 6 月在蓝家湖采自广西壮族自治区贺州市黄田镇油麻岩，隶属于珠江流域贺江水系。

模式标本保藏于广西水产畜牧学校生物标本馆。

副模标本：2010004～2010007(4 尾)，体长 67.1～97.8 mm，采集信息同正模。

图 1　黄田金线鲃(正模标本 2010003，体长 115.0 mm)
Fig. 1　*Sinocyclocheilus huangtianensis* sp. nov. (Holotype 2010003, standard length 115.0 mm)

鉴别特征：新种背鳍末根不分支鳍条柔软，后缘光滑无锯齿，眼正常，侧线鳞为 52～59 枚，侧线上鳞 17～23，侧线下鳞 16～17，鳃耙 9～10，可与属内其他物种相区别。侧线鳞为 52～59 枚，眼径为体长的 4.3%～5.4%，眼间距为体长的 9.2%～9.6%，口裂较小，口裂宽为体长的 6.0%～7.3%，与近似种季氏金线鲃和桂林金线鲃有明显区别。

描述：测量标本 5 尾，全长 84.7～140.0 mm，体长 67.1～115.0 mm。黄田金线鲃数量性状见表 1。

体延长，侧扁。头背交界处的背部隆起不显著，背部轮郭自头部弧形向上延伸，身体最高点在背鳍起点处，之后至尾鳍基部身体高度逐渐下降。腹部轮郭呈向下弯曲的弧形，从吻端下弯至腹部起点，之后逐渐向上，至臀鳍止点后平直至尾鳍基部。

头侧扁，近似圆锥形；前端尖，后端宽而高，头部上缘轮廓斜向后方延伸，稍高于眼上缘。吻端宽而扁平，向前突出，吻长小于眼后头长，头宽略小于头高。鼻孔位于吻与眼的中间，上颌须基部之后，距眼前缘较距吻端稍近，前后鼻孔紧相邻，前鼻孔周缘皮肤形成短管，后缘皮肤向上延伸呈瓣状，后鼻孔椭圆形。眼中等大，眼上缘略低于头背轮廓线，眼间距较宽。口端位，上颌略长于下颌，弧形。唇简单。须 2 对，较长，吻须起点位于前鼻孔之前，后伸超过眼后缘，几乎达前鳃骨后缘，口角须后伸超过前鳃骨后缘。鳃膜在前鳃盖骨后缘垂直线下方连于峡部。

背鳍起点约与腹鳍起点相对，至吻端较尾鳍基稍远，背鳍末根不分支鳍条纤细柔软，后缘无锯齿。胸鳍短，后伸不达腹鳍。腹鳍较长，后伸几乎达肛门。臀鳍紧接肛门之后，其起点距腹鳍起点较尾鳍基为近。尾鳍叉形。

体表被鳞，鳞片细小，幼体鳞片埋于皮下，成体部分个体背部鳞片埋于皮下。侧线鳞稍大于其上、下方鳞片，胸腹部鳞片明显。腹鳍腋部具一枚小腋鳞。侧线完全，在胸鳍上方稍向下弯曲，往后延伸至尾鳍基部的中央。头前面眶上管、头部侧面眶下管和头部下方舌颌管之侧线孔明显。眼下方辐射状感觉管明显。

鳃耙短而圆钝，排列稀疏。下咽齿末端尖而稍钩曲。鳔 2 室，前室椭圆形，后室近圆锥形，前部膨大，后部尖细，前室为后室的 2/3 长。

体色：福尔马林固定后标本体色为灰黑色，背部颜色较深，腹部浅灰色，体中部延平行于背缘有一黑色纵纹，纵纹上有数个黑色圆点；背鳍下方头后延背缘有一列黑色圆点。幼体在侧线下方腹鳍上方的体侧有 2 个黑色圆点。各鳍浅灰色。

词源：新种采集于广西贺州市黄田镇，以地名命名为黄田金线鲃，取采集地黄田 huangtianensis 作为新种种名，中性。

3　讨　论

金线鲃属内存在 4 个主要类群，分别是“季”类、“角”类、“驼背”类和“抚仙”类，这些类群有不同的形态特征，大体占据不同的分布区(Zhao & Zhang, 2009)。本新种具有背鳍末根不分支鳍条柔软，后缘光滑无锯齿；眼睛正常，鳞片中等大，侧线鳞数目通常为 50 左右；胸鳍较短，后伸不超过腹鳍起点；侧线走向不平直等特征，与同分布在贺江水系的季氏金线鲃(*S. jii*), (图 2)及邻近的漓江水系的桂林金线鲃(*S. guilinensis*)(图 3)相近似，应同属“季”类，但新种侧线鳞数 52～59，侧线上鳞 17～23，侧线下鳞 16～17，围尾柄鳞 40～46，第一鳃弓外侧鳃耙 9～10，眼径为体长的 4.3%～5.4%，眼间距为体长的 9.2%～9.6%，口裂较小，口裂宽为体长的 6.0%～7.3%，与这两者有明显区别。新种与相近种季氏金线鲃及桂林金线鲃的比较见表 2。

表 1　黄田金线鲃数量性状(长度单位：mm)

Tab. 1　Morphometrics and meristics of *Sinocyclocheilus huangtianensis* sp. nov. (Length in mm)

性状特征	Characteristics	正模标本 Holotype	范围 Range	平均数 Mean
背鳍条	Dorsal fin rays	iii-7	iii-7	
臀鳍条	Anal fin rays	iii-5	iii-5	
胸鳍条	Pectoral fin rays	i -12	i-12～13	
腹鳍条	Pelvic fin rays	i-8	i-7～8	
第一鳃弓外侧鳃耙	Gill raker	9	9～10	
下咽齿	Pharyngeal teeth	2·3·4～4·3·2	2·3·4～4·3·2	
侧线鳞	Lateral line scales	56	52～59	
侧线上鳞	Scale rows above lateral line	21	17～23	
侧线下鳞	Scale rows below lateral line	16	16～17	
背鳍前鳞	Predorsal scales	45	39～45	
围尾柄鳞	Circumpeduncular scales	44	40～46	
全长	Total length	140.0	84.7～140.0	111.6
体长	Standard length	115.0	67.1～115.0	90.1
头长	Head length	33.5	19.0～33.5	25.4
为体长的%	In % of standard length			
头长	Head length	29.2	27.0～29.2	28.2
体高	Body depth	21.3	21.3～28.2	25.9
背鳍前距	Predorsal length	52.4.	50.7～55.4	52.6
背鳍基长	Dorsal fin base length	12.2	11.6～14.3	12.7
背鳍长	Dorsal fin length	16.9	16.4～20.9	18.2
臀鳍前距	Preanal length	71.1	69.1～73.0	71.1
臀鳍基长	Anal fin base length	9.7	7.8～9.7	8.7
臀鳍长	Anal fin length	16.8	16.3～17.7	17.0
胸鳍前距	Prepectoral length	28.7	26.　～28.7	27.1
胸鳍基长	Pectoral fin base length	3.8	3.8～4.7	4.1
胸鳍长	Pectoral fin length	19.5	17.3～20.7	19.5
腹鳍前距	Prepelvic length	52.6	50.6～53.8	52.1
腹鳍基长	Pelvic fin base length	3.6	3.6～4.5	4.0
腹鳍长	Pelvic fin length	15.1	13.6～16.7	15.6
尾柄长	Caudal-peduncle length	21.5	21.2～23.4	21.9
尾柄高	Caudal-peduncle depth	10.7	10.7～13.1	11.7
头高	Head depth	16.5	16.4～18.2	17.3
头宽	Head width	15.9	14.9～16.2	15.7
吻长	Snout length	8.7	8.7～9.8	9.3
眼径	Eye diameter	5.4	4.3～5.4	5.0
眼间距	Interorbital width	9.5	9.2～9.6	9.4
前鼻孔前距	Prenostril length	5.6	5.2～5.7	5.5
后鼻孔间距	Width between Poster nostrils	6.1	5.9～6.8	6.3
上颌长	Upper jaw length	7.6	6.3～7.9	6.5
下颌长	Lower jaw length	7.4	6.3～7.4	6.8
口裂宽	Mouth width	10.8	8.8～10.8	9.3
吻须长	Rostral barbel length	16.5	10.7～16.5	13.1
口角须长	Mouth corner barbel length	16.4	13.7～16.4	14.6

图 2　季氏金线鲃(正模标本 ASIZB 62726，体长 123.6 mm)
Fig. 2　*Sinocyclocheilu jii* (Holotype ASIZB 62726, standard length123.6 mm)

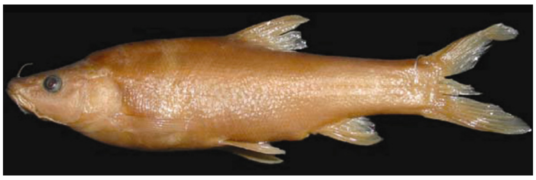

图 3　桂林金线鲃(正模标本　ASIZB 113753，体长 107.3 mm)
Fig. 3　*Sinocyclocheilu guilinensis*(Holotype, ASIZB 113753, standard length 107.3 mm)

表 2　新种与相近种季氏金线鲃及桂林金线鲃的比较(长度单位：mm)
Tab. 2　Comparison of new species , *Sinocyclocheilu jii* and *S. guilinensis* (Length in mm)

性状特征	Characteristics	黄田金线鲃 *S. huangtianensis* sp. nov.	季氏金线鲃 *S. jii*	桂林金线鲃 *S. guilinensis*
侧线鳞	Lateral line scales	52～59	43～53	47～52
侧线上鳞	Up lateral line scales	17～23	27～29	19～20
侧线下鳞	Down lateral line scales	16～17	15～17	11～12
围尾柄鳞	Circumpeduncular scales	40～46	46～50	34～36
鳃耙	Gill raker	9～10	6～7	8～11
眼径/体长	Eye diameter/SL	4.3%～5.4%	7.2%～8.6%	7.1%～9.1%
眼间距/体长	Interorbital width /SL	9.2%～9.6%	6.4%～7.8%	6.1%～7.1%
口裂宽/体长	Mouth width/SL	6.0%～7.3%	7.7%～8.4%	7.9%～8.4%
分布	Distribution	广西贺州市黄田镇	广西富川县、恭城县观音乡	广西桂林市

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广西岭鳅属鱼类一新种——罗城岭鳅 (鲤形目：爬鳅科)

BACK

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摘要：2008 年 9 月，在广西壮族自治区罗城县天河镇附近一洞穴采集到一批条鳅亚科鱼类标本。经鉴定，为岭鳅属(*Oreonectes*)一新种。新种与岭鳅属的其他已知种类在以下组合特征上有区别：背鳍条 3, 7；臀鳍条 2, 5；胸鳍条 1, 11～12；腹鳍条 1, 7；尾鳍分枝鳍条为 14～16。头平扁；眼正常；下唇表面具浅皱。腹鳍起点位于背鳍起点垂线下方之前，尾柄上、下缘无明显鳍褶；尾鳍后缘平截。体侧具不明显的细小鳞片，或鳞片隐于皮下。头部无侧线感觉系统管孔。成体粉红色，无色素，各鳍透明；浸泡标本体呈乳黄色，不透明，通体无色斑。

关键词：广西；新种；爬鳅科；岭鳅属
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A new loach, *Oreonectes luochengensis* sp. nov. (Cypriniformes: Balitoridae) from Guangxi, China

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Abstract: A cave-dwelling loach, *Oreonectes luochengensis* sp. nov. has been described based on collections from a cave in Tianhe town, Luocheng, Guangxi, China in September 2008. It can be distinguished from all known *Oreonectes* species by the following combination of characters: dorsal-fin rays 3, 7; anal-fin rays 2, 5; pectoral-fin rays 1, 11−12; pelvic-fin rays 1, 7 and 14−16 branched caudal-fin rays; head compressed; eyes present; surface of lower lip covered with shallow longitudinal groove; dorsal-fin origin posterior to vertical line of pelvic-fin origin; caudal peduncle without caudal-adipose keels; edge of caudal fin truncation; tiny scales present under skin; no cephalic lateral-line system; body pink in living status, without pigments in adult, after fixed in formalin, body yellowish, non-transparent, no markings on body side.

Key words: Guangxi; New species; Balitoridae; *Oreonectes*

岭鳅属(*Oreonectes*)鱼类隶属于鲤形目(Cypriniformes)爬鳅科(Balitoridae)条鳅亚科(Nemacheilinae)(Nelson, 2006)。目前，岭鳅属共记录有 8 个种(Romero et al, 2009; Huang et al, 2009)。岭鳅属鱼类主要分布在中国西南，国外仅记录分布于越南北部的 Quang Ninh 省(Kottelat, 2001)。本属鱼类以平头岭鳅(*Oreonectes platycephalus* Günther)分布最为广泛，历史记录分布于广东、广西和越南北部地区(Zheng, 1989; Kottelat, 2001; Fisheries Institute of Guangxi Zhuang Autonomous Region, Institute of Zoology, Chinese Academy of Science, 2006)。本属其余 7 种都分布在广西，为广西特有种，且都为喀斯特地貌环境中地下河洞穴种类(Fisheries Institute of Guangxi Zhuang Autonomous Region, Institute of Zoology, Chinese Academy of Science, 2006; Du et al, 2008; Huang et al, 2009)。岭鳅属鱼类前、后鼻孔分开一短距，前鼻孔末端延长呈须状；头平扁，关宽大于头高；尾柄短、侧扁；

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无侧线或侧线不完全(Zhu, 1989; Du et al, 2008)。2008 年 9 月，在广西壮族自治区罗城县天河镇附近一洞穴采集到一批条鳅亚科鱼类标，经鉴定，这批标本为岭鳅属一新种。

1 材料与方法

研究标本均用 10%甲醛溶液浸泡、保存。标本依 Zhu（1989 ）、Du et al（2008) 进行鉴定；标本依 Kottelat (1990) 进行测量。

2 结 果

2.1 罗城岭鳅，新种 *Oreonectes luochengensis* sp. nov (图 1、2)

正模标本 KIZ 2010003073，体长 74.9 mm，2008 年 9 月采自广西壮族自治区罗城县天河镇东南方向约 2 km 一洞穴，天河支流，属西江水系。采集人：蓝家湖。正模标本保存在中国科学院昆明动物研究所鱼类标本库。

图 1 罗城岭鳅副(模标本 KIZ2010003076, 75.0 mm)

Fig. 1 *Oreonectes luochengensis* sp. nov. (Paratype KIZ2010003076, 75.0 mm)

图 2 罗城岭鳅活体照

Fig. 2 Living status of *Oreonectes luochengensis* sp. nov.

副模标本 7 尾，KIZ 2010003074～2010003077 (4 尾标本保存在中国科学院昆明动物研究所鱼类标本库)，08090054～08090055 和 08090064(3 尾标本保存在广西壮族自治区水产研究所)，体长 64.6～80.0 mm，标本信息与正模标本相同。

2.2 鉴别特征

背鳍条 3, 7；臀鳍条 2, 5；胸鳍条 1, 11～12；腹鳍条 1，7；尾鳍分枝鳍条为 14～16。头平扁；眼正常；下唇表面具浅皱。腹鳍起点位于背鳍起点垂直下方之前，尾柄上、下缘无明显鳍褶；尾鳍后缘平截。体侧具不明显的细小鳞片，或隐于皮下。头部无侧线感觉系统。成体通体一色，无色素，浸泡标本体呈乳黄色，不透明，通体无色斑。

2.3 形态描述

罗城岭鳅的测量性状见表 1。身体延长，前躯呈圆筒形，后躯侧扁。尾柄高，侧扁。头平扁，顶部宽平。吻圆钝，吻长小于眼后头长。口下位。下唇表面具浅皱。上颌弧形，下颌匙状。须 3 对，内侧吻须后伸可达后鼻孔的垂直下方；外侧吻须和颌须后伸都可达眼后缘的垂直下方。前、后鼻孔分开一短距离，前鼻孔位于管状突起中，管状突起末端延长成须状，鼻须后压可达后鼻孔。眼存在，正常。头部和胸腹部无鳞，体侧鳞片不明显，隐于皮下。侧线不完全，具 6～13 个侧线孔。

表 1 罗城岭鳅的测量比例性状

Tab. 1 Proportional measurements of *Oreonectes luochengensis* sp. nov.

性状 Characters	*n*=8		
	范围 Range(mm)	平均值 Mean	标准差 *SD*
体长 Standard length	64.6～80.0	72.3	4.9
头长 Head length	9.25～13.4	11.5	1.3
与体长相比的百分数 Percentage of standard length			
体高 Body depth	14.3～17.5	16.0	1.1
头长 Head length	19.8～22.4	20.6	0.8
尾柄长 Caudal-peduncle length	13.6～15.1	14.5	0.5
尾柄高 Caudal-peduncle depth	9.8～12.1	11.1	0.8
前背长 Distance between snout and dorsal-fin origin	56.9～60.1	58.2	1.2
前腹长 Distance between snout and pelvic-fin origin	52.9～56.3	54.6	1.1
胸腹间距 Distance between pectoral-fin origin and pelvic-fin origin	32.7～37.2	34.8	1.3
腹臀间距 Distance between pelvic-fin origin and anal-fin origin	22.1～26.9	24.3	1.6
与头长相比的百分数 Percentage of head length			
吻长 Snout length	38.6～45.8	41.6	2.3
眼径 Eye diameter	11.2～14.3	12.5	1.2
眼间距 Interorbital width	44.0～51.4	48.5	2.5
头宽(后鼻孔处) Head width (between posterior nares)	32.5～39.2	35.8	2.4
最大头宽 Maximum head width	70.5～77.7	73.7	2.6
与尾柄长相比的百分数 Percentage of caudal-peduncle length			
尾柄高 Caudal-peduncle depth	65.4～85.2	76.7	7.1

背鳍短小，后缘圆弧形，位置较后，具 7 根分枝鳍条。胸鳍分枝鳍条 11～12，外周缘常呈锯齿状缺刻，长约为胸、腹鳍基部起点之间距离的一半。腹鳍具 7 根分枝鳍条，位置较前，基部相对于背鳍起点的前方，腹鳍末端后伸不达肛门。臀鳍起点约与背鳍后缘相对，距肛门约 2 倍眼径的距离。尾鳍后缘平截，具 14～16 根分枝鳍条。尾柄上、下无明显的鳍褶。胃“U”形，肠直。鳔分两室，前室包裹于一骨质鳔囊中，骨质鳔囊侧囊的后壁为膜质，后室为发达的膜质室，游离于腹腔中，通过一短管与前室相连，短管末端近胸鳍末端，鳔后室末端近腹鳍起点。

活体标本全身粉红色、半透明，体侧偶可看见血管，身体无色斑 (图 2)。偶见小个体标本体色略深，具色素。经福尔马林浸泡的标本，体呈乳黄色，不透明，各鳍白色，身体无色斑。

2.4 分布

目前，本种已知的分布点仅为广西壮族自治区罗城县天河镇东南方向沿天河镇至四把镇公路，距天河镇约2 km处路边的一洞穴中，属西江水系(图3)。

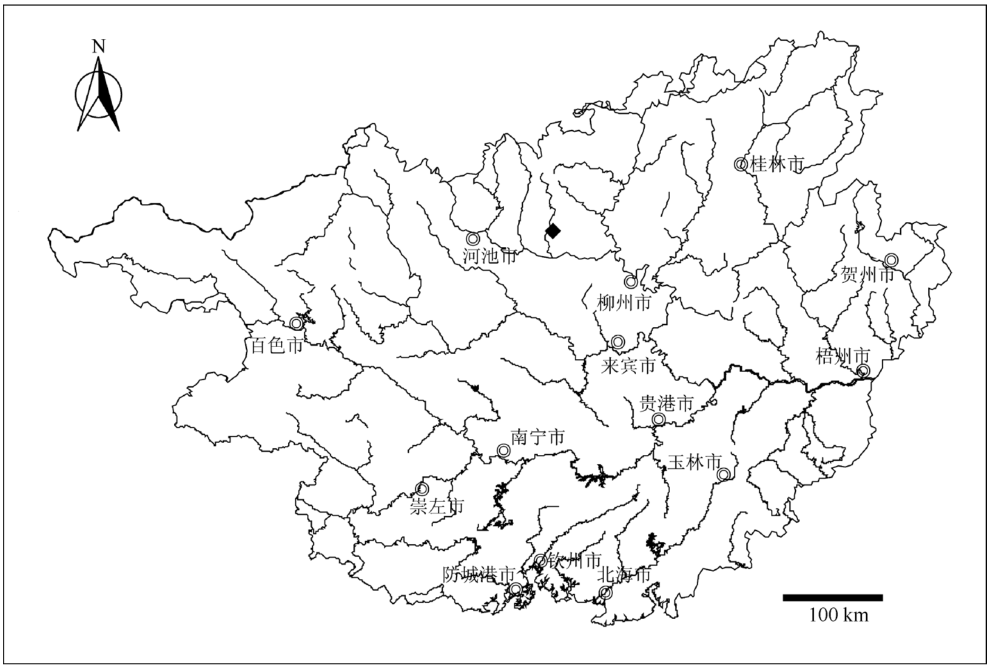

图 3 罗城岭鳅(◆)在广西壮族自治区的分布示意图

Fig. 3 Map showing the collection site of *Oreonectes luochengensis* sp. nov. (◆) in Guangxi Zhuang Autonomous Region

2.5 词源

“*luochengensis*”，源自于罗城(Luo Cheng)的汉语拼音。以本新种的模式产地县名来命名。

2.6 生境与生态

本种喜欢在下雨水涨后游出到洞外周边水体活动，模式采集地仅有罗城岭鳅，无其他鱼类分布。解剖了采自 2008 年 9 月的一尾标本(标本号 08090039，体长 73.5 mm)，为雌性，腹中明显可见发育到 III～IV 的卵。

3 讨 论

Du et al (2008)认为岭鳅属鱼类最明显的特征为前、后鼻孔分开一短距离，前鼻孔在一短的管状突起中，短管状突起的顶端延长成须状；头平扁，前躯近圆筒形；尾柄短、侧扁；无侧线或侧线不完全。本新种体型结构与岭鳅属鱼类的特征相符，隶属于岭鳅属。

依 Du et al (2008)对岭鳅属鱼类的种组划分，罗城岭鳅归属于以平头岭鳅为代表种的圆尾种组。圆尾种组与叉尾种组依尾形的差异很容易相互区别开来。目前，叉尾种组的岭鳅属鱼类共 4 种，分别是叉尾岭鳅(*Oreonectes furcocaudalis* Zhu & Cao)、小眼岭鳅(*O. microphthalmus* Du, Chen & Yang)、大鳞岭鳅(*O. macrolepis* Huang, Chen & Yang)和透明岭鳅(*Oreonectes translucens* Zhang, Zhao & Zhang)。圆尾种组共 5 种，分别是平头岭鳅(*O.*

platycephalus Günther)、无眼岭鳅(*O. anphthalmus* Zheng)、多斑岭鳅(*O. polystigmus* Du, Chen & Yang)、后鳍岭鳅(*O. retrodorsalis* Lan, Yang & Chen)和罗城岭鳅，其中，无眼岭鳅和透明岭鳅为盲鱼，很容易与罗城岭鳅相区别开来。多斑岭鳅以其体表具独特不规则斑纹和尾鳍后缘圆弧形与罗城岭鳅(活体标本全身乳白色、呈半透明状，体侧偶可看见血管，身体无色斑，尾鳍缘平截)相区别。后鳍岭鳅尾鳍后缘凹入，体型较少，尾柄上、下具明显的软鳍褶(Lan et al, 1995;　Du et al, 2008)，这些特征可以与罗城岭鳅(尾鳍后缘平截，体型较大，尾柄上、下无明显软鳍褶)相区别。罗城岭鳅与平头岭鳅 (图 4；图 5)体型最为相近，但它们体色差异较大。平头岭鳅除头部外，通体被鳞，而罗城岭鳅体表大部分鳞片不显，仅残留退化程度不一的鳞片隐于皮下。平头岭鳅胸鳍分枝鳍条数为 10，而罗城岭鳅胸鳍分枝鳍条数为 11～12。罗城岭鳅鳔后室发达，游离于腹腔中(平头岭鳅鳔后室明显退化)。罗城岭鳅胸鳍后伸不达胸鳍起点与腹鳍起点间距的 1/2(平头岭鳅胸鳍后伸超过胸鳍起点与腹鳍起点间距的 1/2)。罗城岭鳅尾鳍外缘平截(平头岭鳅尾鳍外缘圆弧形)。

图 4　平头岭鳅侧面观 (04040114，体长 77.0 mm)
Fig. 4　Lateral view of *Oreonectes platycephalus* (77.0 mm SL)

图 5　平头岭鳅活体照
Fig. 5　Living status of *Oreonectes platycephalus*

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滇池大型无脊椎动物的群落演变与成因分析

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摘要：该文综合滇池大型无脊椎动物的历史资料，并结合 2009—2010 年的现场调查数据，对其群落演替进行了研究，并对群落衰退的成因进行了探讨。物种数下降明显，由 20 世纪 80 年代的 57 种降为现在的 32 种，群落的物种损失率高达 44%。其中软体动物损失率高达 75%；其次是水生昆虫（39%）。滇池全湖底栖动物密度为 1 776 ind/m^2（其中寡毛类 1 706 ind/m^2；摇蚊科 68 ind/m^2）。近 20 年滇池全湖底栖动物的丰度比较发现，寡毛类的密度和生物量呈一种先急剧上升，而后明显下降的过程，而摇蚊科的密度和生物量呈现出减少的趋势。寡毛类中的耐污种相对丰度增加，如霍甫水丝蚓（*Limnodrilus hoffmeisteri*）成为绝对优势种，其平均相对丰度达到了 74.1%。摇蚊科相对丰度减少，以前广泛分布的异腹鳃摇蚊（*Einfeldia* sp.）基本消失，取而代之的是羽摇蚊（*Chironomus plumosus*）、细长摇蚊（*Ch. attenuatus*）、中国长足摇蚊（*Tanypus chinensis*）等耐污种；软体动物种类变得单一，许多高原湖泊特有的软体动物均已消失，螺蛳（*Margarya melanioides*）、牟氏螺蛳（*M. mondi*）、光肋螺蛳（*M. mansugi*）在 2009 年被世界自然保护联盟列入了极危物种，滇池圆田螺（*Cipangopaludina dianchiensis*）也被列入了濒危物种。滇池的 Shannon-Wiener 多样性指数显著降低，尤其是草海物种多样性从 20 世纪 50 年代的 2.70 降到现在的 0.30。半个多世纪以来总氮、总磷与物种数和多样性呈现显著负相关。底栖动物群落衰退的成因主要是生境破坏、水质恶化、蓝藻爆发、沉水植物消失、种质库匮乏等。

关键词：滇池；大型无脊椎动物；群落演变；成因分析
中图分类号：Q959.1(74)；Q958.1；X174(74)　　**文献标志码**：A　　**文章编号**：0254-5853-(2011)02-0212-10

Diianchi Lake macroinvertebrate community succession trends and retrogressive analysis

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Abstract: Historical records and data from yield surveys conducted in 2009 and 2010 were used to investigate macroinvertebrate community succession trends in Dianchi Lake. Species richness has declined from 57 in the 1980s to 32 in 2010, representing a species loss of 44%. Among the major benthic groups, the highest rate of loss was recorded for mollusks (75%) and aquatic insects (39%). Surveys in 2009 and 2010 across the lake revealed that the total density was 1776 ind/m^2, comprising oligochaetes (1706 ind/m^2) and chironomids (68 ind/m^2). Over a nearly twenty-year span (1992 − 2010), the density and biomass of oligochaetes first increased sharply (1992 – 2002) and then declined gradually (2002 – 2010). Further, chironomids have decreased gradually while the proportion of abundant species has increased. *Limnodrilus hoffmeisteri* became the sole dominant species with an average relative abundance of 74.1%. Cosmopolitan species, such as *Einfeldia* sp., disappeared across the lake; instead, tolerant species such as *Chironomus plumosus*, *Ch. attenuatus* and *Tanypus chinensis* became the common. Mollusk community structure has become simpler and many native species have gone extinct. Species of concern include *Margarya melanioides*, *M. mondi*, *M. mansugi* and *Cipangopaludina dianchiensis*, all rated as critically endangered by the IUCN. We found that the Shannon-Wiener index declined in Dianchi Lake, particularly in Caohai Lake, from 2.70 in the 1950s to 0.30 in 2009 and 2010. Species richness and biodiversity was significantly negative correlated with total phosphorus and total nitrogen. Factors responsible for the benthic community retrogression described here include habitat destruction, lowering of water quality, outbreaks of

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blue-green algae, extinction of submerged plants and lack of germplasm resources.

Key words: Dianchi Lake; Macroinvertebrate; Community succession; Retrogressive analysis

滇池系云贵高原上的一个大型浅水湖泊，滇池底栖动物的现状令人堪忧。近几十年来，随着湖区经济的快速发展和人口的急剧增长，人类对其自然资源的开发不断加剧，使其生态环境逐渐恶化，富营养化进程加剧，水质呈不断下降趋势，草海和外海都是劣Ⅴ类水体，呈严重富营养化状态。为此，国家将滇池污染治理列为全国重点治理的“三河三湖”之一（Zhe, 2002）。富营养化影响底栖动物群落结构和多样性（Gong et al, 2001）；有机物的增加会导致淤积、底质改变、缺氧。这些都影响一些底栖动物的分布（Graneli & Solander, 1988）。近年来，滇池大量物种消失，耐污种成为了优势种，整个生态系统出现了危机。滇池水环境退化与物种多样性丧失呈双向恶化效应，物种多样性重建是滇池生态恢复的重要指标（Luo et al, 2006）。本文根据作者在 2009—2010 年对滇池全湖底栖动物的调查研究结果，结合以往历次研究资料，分析了半个多世纪以来滇池底栖动物群落结构的变化及其所指示的湖泊环境演变，阐明人类活动对底栖生物群落结构的影响及其机理，从而为科学利用和保护滇池提供依据。

1　研究区域概况

滇池属金沙江水系，包括草海和外海两部分，为昆明市所辖，位于 24°40′～25°02′N、102°37′～102°48′E之间，湖面高程1 885 m；湖体南北最长39 km，东西最宽 12.5 km，最窄 2.44 km，湖岸线长 151.2 km，湖面面积298.4 km^2，平均水深4.1 m，最大水深 8 m，水容量约 12.9 亿立方米（海拔为 1 886.5 m），属于高原构造型亚热带石灰岩富营养型湖（Yang & Yang, 1985）。滇池呈南北向分布，湖体略呈弓形，弓背向东，东北部有一天然沙堤，长约4 km，将滇池分为南北两部分，称为外海和草海（图 1）。

2　材料与方法

2.1　数据来源

数据来源于滇池大型底栖动物的历史资料（Zhang, 1948; Zhang & Qi, 1949; Zhang &Wu, 1983; Wang, 1985; Wang et al, 2007; Luo et al, 2006），以及本次的调查结果。滇池历年的理化指标自 1985 年及以后来源于《云南省环境状况公报》，1985 年以前的理化指标据参考文献：Yu et al, 2000; Li, 1963。本次调查共设30个采样点，其中外海24个，草海6个（图 1）。底栖动物的采集使用 0.0625 m^2 的改良彼得生采样器，软体动物的采集主要使用三角拖网。动物标本的鉴定据参考文献：Epler, 2001; Brinkhurst, 1986; Liu et al, 1979。

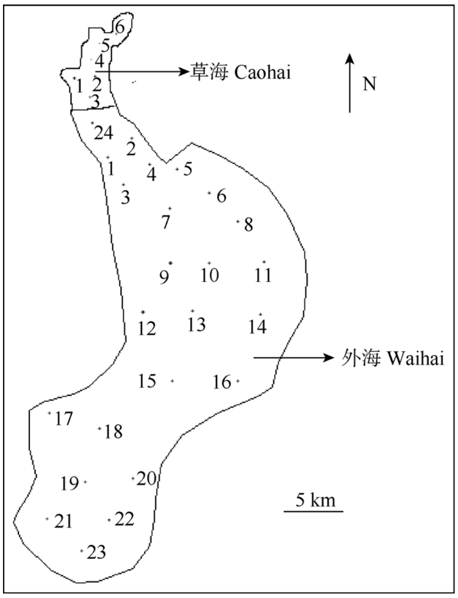

图 1　2009—2010 年滇池大型无脊椎动物采样点分布图
Fig. 1　The sampling stations of macroinvertebrates in Dinachi Lake in 2009-2010

2.2　数据处理

底栖动物的物种多样性的计算采用 Shannon-Wiener 指数计算底栖动物的多样性。具体计算采用 Excel 软件和 biodiversity tool 工具进行。统计分析用 SPSS 软件，群落结构及其与环境关系采用线性回归进行分析。物种损失率的计算公式为 $P=（S-S_i）/S_i$，式中 S 为本次调查的物种数，S_i 为 i 年前的物种数。Shannon-Wiener 多样性指数，即 $H=-\sum\{(n_i/N)\ln(n_i/N)\}$。式中 N 为总密度，n_i 为物种 i 的密度。

3　结果与分析

3.1　群落结构的演变

3.1.1　物种数　自20世纪70年代以来，滇池共记

录大型无脊椎动物 85 种，隶属于 3 门 6 纲 28 科(附表 1)。20 世纪 40 年代记录 51 种, 70 年代 33 种, 80 年代 57 种, 90 年代 21 种, 2002 年 13 种。从 20 世纪 40 年代到 80 年代总体上呈现出一种稳定的趋势，可是从 20 世纪 80 年代到现在显著降低（图 2）。

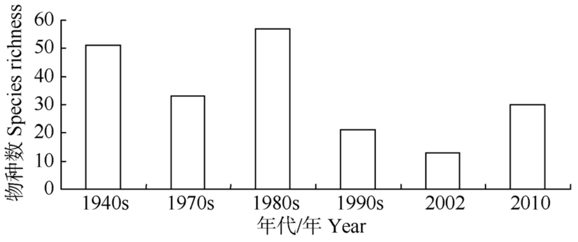

图 2　半个多世纪滇池大型底栖动物物种丰度的比较
Fig. 2　Comparison of species richness of macroinvertebrate in Dianchi Lake across half a century

2009—2010 年共记录到大型底栖动物 32 种，隶属 3 门 4 纲 9 科 26 属（附表 1）。其中寡毛纲 10 种，昆虫纲 14 种，软体动物 6 种，蛭纲 1 种，甲壳纲 1 种。其中百陶溪毛蚓（*Patamothrix bedoti*）为滇池首次发现。与 20 世纪 80 年代相比，本次调查表明滇池大型无脊椎动物群落的物种损失率高达 44%。其中软体动物损失率高达 75%，其次是水生昆虫（39%）。滇池所存物种主要由极度耐污的寡毛类——霍甫水丝蚓（*Limnodrilus hoffmeisteri*）、正颤蚓（*Tubifex tubifex*）、苏氏尾鳃蚓（*Branchiura sowerbyi*）和摇蚊科幼虫——羽摇蚊（*Chironomus plumosus*）、细长摇蚊（*Ch. attenuatus*）等组成，高原湖泊特有的软体动物中除螺蛳（*Margarya melanioides*）、牟氏螺蛳（*M. mondi*）、光肋螺蛳（*M. mansugi*）、滇池圆田螺（*Cipangopaludina dianchiensis*）外均消失殆尽。

3.1.2　优势类群　寡毛类物种数增加，由 20 世纪 70 年代在全湖广泛分布的 1 种（苏氏尾鳃蚓）增加到现在的 10 种，其中霍甫水丝蚓为绝对优势种，平均相对丰度达到了 74.1%，其平均密度为 1 502 ind/m^2，占总密度的 85.7%；其次为正颤蚓，其平均相对丰度为 9.3%，而苏氏尾鳃蚓的平均相对丰度只有 4.2%。在水生昆虫中，摇蚊科的种类增加明显，由 20 世纪 80 年代的 4 种增加到现在的 12 种，但是在水生昆虫中其他类群的种类渐趋消亡，以前广泛分布的水甲科（Haliplidae）、鼓甲科（Gyrinidae）、水龟虫科（Hydrophilidae）、仰游蝽科（Notonectidae）等的种类现在已没有发现。Wang（1985）在 1982—1983 年的调查中发现，在全湖广泛分布的摇蚊科只有羽摇蚊，另外异腹鳃摇蚊（*Einfeldia* sp.）也有广泛分布。在本次调查中发现全湖的绝对优势种仍为羽摇蚊，其平均相对丰度为 2.7%，平均密度为 31 ind/m^2，占总密度的 1.7%。另外细长摇蚊、中国长足摇蚊（*Tanypus chinensis*）也较多，可是却没有发现在 20 世纪 80 年代分布广泛的异腹鳃摇蚊。

软体动物方面，20 世纪 70 年代和 80 年代的物种数差别不大，大约有 24 种（Zhang & Wu, 1983;Wang, 1985）。可是本次调查只发现 6 种。根据 1997 年 Huang et al（1997）对滇池的调查，湖中软体动物十分丰富，瓣鳃类除无齿蚌（*Anodonta* sp.）和河砚（*Corbicula fluninea*）外，尚有凝菱珠蚌（*Rhombunopsis* sp.）、相珠蚌（*Unionea* sp.）等，可是在本次调查中却只发现无齿蚌一种。软体动物的方格短沟蜷（*Semisulcospira cancellata*）过去报道在滇池中有很大的群体数量，但这次只采到螺壳，也属于绝迹或即将绝迹的种类。Wang（1985）在 1982—1983 年对滇池进行的调查中发现软体动物中的腹足类有 19 种，可是在 2009 年的调查中却只发现 5 种，扁卷螺科（Planorbidae）只采到空壳，以前广泛分布的特有种云南萝卜螺（*Radxi yunnanensis*）在此次调查中未发现，高原湖泊特有的软体动物如螺蛳、牟氏螺蛳、光肋螺蛳在 2009 年被世界自然保护联盟（IUCN）列入了极危物种（critically endangered, CR），滇池圆田螺也被列入了濒危物种（endangered, EN）（http://www.iucnredlist.org）。

3.1.3　密度和生物量　由于缺乏滇池软体动物的定量数据，本节主要分析寡毛类和摇蚊科现存量的演变趋势（图 3）。20 世纪 90 年代初底栖动物的丰度还相对较少，平均密度和生物量分别为 696 ind/m^2 和 14.13 g/m^2，其中寡毛类密度和生物量分别为 138 ind/m^2 和 6.78 g/m^2（分别占总丰度的 19.8% 和 48%），摇蚊科密度和生物量分别为 558 ind/m^2 和 7.35 g/m^2（80.2%和 52%）。而 2002 年底栖动物的丰度达到峰值，其密度和生物量分别为 5 017 ind/m^2 和 22.2 g/m^2，其中寡毛类密度和生物量分别为 4609 ind/m^2 和 18.02 g/m^2（分别占总丰度的 91.9% 和 81.2%），摇蚊科密度和生物量分别为 408 ind/m^2 和 4.18 g/m^2（分别占总丰度的 8.1%和 8.8%）。本次一年的调查结果，显示滇池全湖底栖动物密度和生物量分别为 1 776 ind/m^2 和 3.43 g/m^2，其中寡毛类密度和生物量分别为 1706 ind/m^2 和 2.83 g/m^2（分

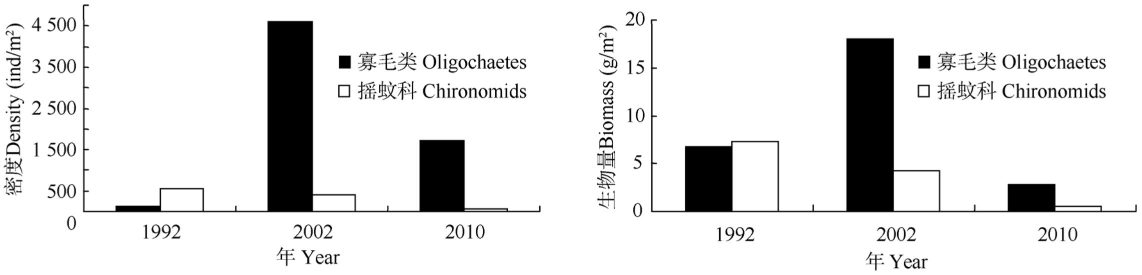

图 3　近 20 年滇池大型底栖动物主要类群丰度的比较

Fig. 3　Comparison of abundance of main macroinvertebrate groups in Dianchi Lake across nearly twenty-year span

别占总丰度的 96.1%和 82.6%)，摇蚊科密度和生物量分别为 68 ind/m^2 和 0.60 g/m^2（分别占总丰度的 3.8%和 17.4%）。

3.1.4　物种多样性　如图 4 所示，滇池草海、外海的物种多样性有逐渐恶化的趋势，尤其是草海，物种多样性指数（Shannon-Wiener index）从 20 世纪 50 年代的 2.70 下降到 2010 年的 0.30，滇池外海的物种多样性指数也由 20 世纪 60 年代的 1.08 降到 2010 年的 0.67。

3.2　群落结构与水质的关系

结合半个多世纪以来滇池外海的总氮（TN）、总磷（TP），分别与物种数和 Shannon-Winner 多样性指数进行分析，发现它们彼此都呈显著负相关（图 5）。

4　讨　论

4.1　滇池大型无脊椎动物的演变

1948 和 1949 两年张玺等曾报道无脊椎动物 51 种，包括 4 种海绵动物（*Spongilla carteri, Spongilla* sp., *Eplydatia fluyiatilia* 和 *Efydatia robusta*）和 2 种腔肠动物（*Hydra vividis* 和 *Hydra vulgari*）。方格短沟蜷在滇池中也有很大的群体数量，椎实螺科（Lymnaeidae）的云南萝卜螺在全湖普遍分布，滇池中螺蛳属（*Margarya*）有 6 种，其他螺类 10 种（Zhang, 1948; Zhang & Qi, 1949）。在 1977 年的调查中，只有 33 种，且淡水海绵动物、腔肠动物已绝

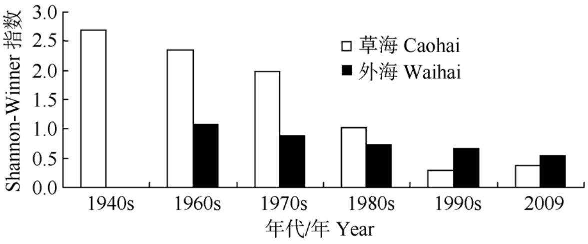

图 4　滇池大型底栖动物多样性的比较

Fig. 4　Comparison of Shannon-Wiener value of macroinvertebrate in Dianchi Lake

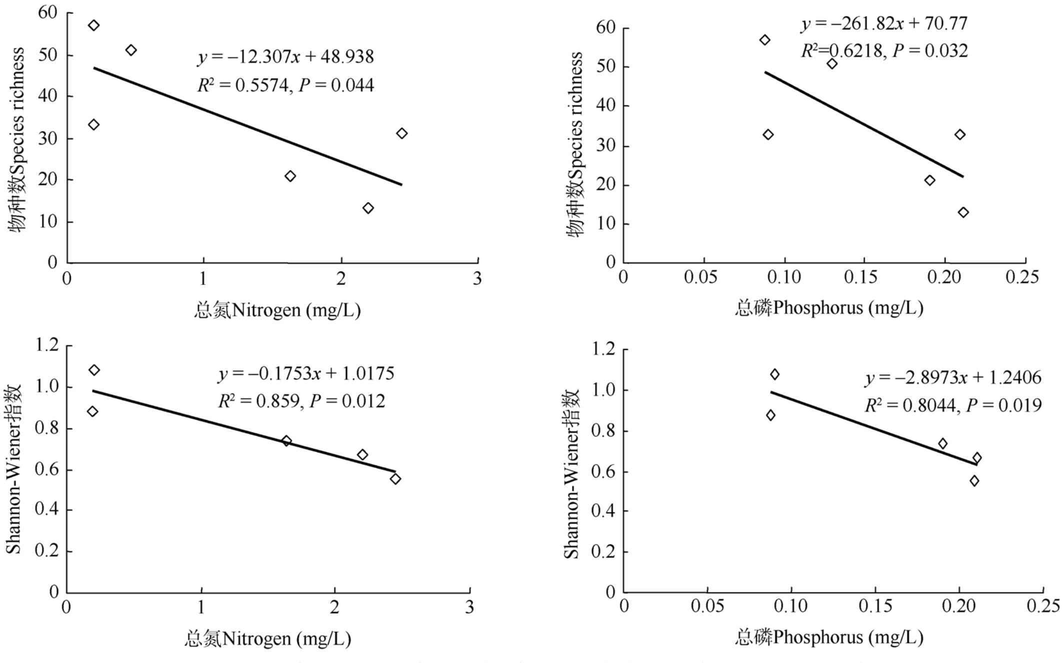

图 5　半个多世纪以来滇池物种数和多样性与总氮和总磷的关系

Fig. 5　The relationship between TN, TP and biodiversity, species richness of macroinvertebrate in Dianchi Lake across half a century

迹，云南萝卜螺除在深水区可以采到标本外很难见到，螺蛳属只发现两种，黑螺科（Melaniidae）的方格短沟蜷已经很难采到（Zhang & Wu, 1983）。1982—1983 年的调查共发现滇池的底栖动物有 57 种（Wang, 1985）。从这次调查中可以看出，滇池无脊椎动物的类组成已发生了较大变化。软体动物曾报道共 55 种，这次调查只采到 24 种，种类和数量明显减少，其中以田螺科、黑螺科最为显著，许多种类趋向消亡；在节肢动物中日本沼虾（*Macrobrachium nipponense*）、羽摇蚊、卵形沼梭成为全湖浅水区的优势种类；寡毛类变化不大，优势种仍为苏氏尾鳃蚓。1995 年的调查中共采到底栖动物 21 种，其中环节动物 4 种，节肢动物 5 种，软体动物 l2 种（大部分为空螺壳），优势类群主要为摇蚊幼虫和寡毛类，结构趋向单一化（Luo et al, 2006）。2001—2002 年王丽珍等根据滇池 6 次采样的定量分析鉴定结果，共获得底栖动物 5 科 9 属 13 种，其中环节动物 2 科 4 属 7 种，摇蚊科幼虫 4 属 4 种，甲壳动物 1 种（Wang et al, 2007）。

物种数从 20 世纪 40 年代到 80 年代总体上呈现出一种稳定的趋势，本次调查的物种数要比上世纪 90 年代和 2002 年多，主要是本次调查更为全面，种类鉴定也更为准确。总体上从 20 世纪 80 年代到现在物种数有降低的趋势，原因可能是滇池水质自 20 世纪 80 年代以来逐渐恶化（Liu, 1999），滇池水环境退化与区域内物种多样性的丧失呈双向恶化的趋势（Luo et al, 2006）。一般底栖动物多样性与总氮（TN）、总磷（TP）呈负相关（Chen et al, 1980; Gong, 2002）。近半个世纪对滇池大型无脊椎动物的研究结果表明，寡毛类的物种数和丰度都有很大的增加，增加的主要为一些耐污种，如霍甫水丝蚓、正颤蚓等。水生昆虫中除了摇蚊科的种类数增加外，其他科的种类渐趋消亡。摇蚊科也主要增加了一些耐污种，如丰度仅次于羽摇蚊的细长摇蚊、中国长足摇蚊等。软体动物的种类数明显减少，特有的云南萝卜螺消失，高原湖泊特有的螺蛳属的几个种和滇池圆田螺都处于极危状态。

近 20 年滇池全湖底栖动物的丰度演替显示，寡毛类的密度和生物量呈一种先急剧上升，而后明显下降的过程，而摇蚊科的密度和生物量呈现一种减少的趋势。随着湖泊富营养化进程的加剧，寡毛类和摇蚊科对此作出了两种不同的响应。底质可能是决定大型底栖底栖动物群落结构最重要的因素（Beisel et al, 1998）。一般地，底栖动物的现存量与底质的稳定性和有机质含量有密切关系（Barmuta, 1989; Quinn & Hickey, 1994）。底质的有机物主要来自于浮游藻类、大型水生植物、动物及陆地植被，滇池的蓝藻爆发、水生植物死亡等大大增加了底质的有机物。2009—2010 一年的采样情况也发现滇池的底泥主要为黑色的富含有机质的淤泥。相比有机物较少的底质，寡毛类在富含有机物的淤泥底质中的数目要多一些（Sauter & Gude, 1996），但是有机物过于丰富的底质中缺氧，底栖动物的丰度将明显下降（Graneli & Solander, 1988）。而摇蚊科的耐污能力要差一些，遭受有机污染的水体中，底质环境的溶氧常处于相对较低水平，这对于生活在这种环境中的底栖动物来说，溶氧明显地成为它们的限制因子，多数种类因不适应这种环境而逐渐消失，摇蚊科幼虫和寡毛类成为优势类群，当缺氧变得更为严峻时，寡毛类成为惟一的优势类群，如果长时间的缺氧，底栖动物将完全消失（Famme & Knudsen, 1985; Milbrink, 1994）。

4.2 大型无脊椎动物衰退的成因

4.2.1 生境破坏 环湖自然湿地不仅对入湖前的污水起到净化作用，对湖内水生植被的恢复也具有重要作用（Li et al, 2003）。滇池经过 70 年代的“围海造田”，造成大规模湿地被破坏，据不完全统计，围海造田共使滇池水面减少 21.8 km^2。80 年代和 90 年代又沿滇池修筑起了 124 km 长的防护堤，使滇池外海沿岸带天然湿地系统被毁，滇池丧失了沿岸带所特有的生境多样性。一般认为，沿岸带底栖动物较深水带有更高的多样性、现存量和生产力（Chen et al, 1980）。沿岸带是水陆生态交错带的一种类型，是指相邻的陆地生态系统与水域生态系统之间的过渡带（Yin, 1995），历来是人类活动最集中的场所，也是地球上最脆弱的湿地生态系统之一。湖滨带的功能主要表现为湖滨水陆交错带内生物或非生物因素的相互作用，对交错带内能量流动和物质循环的调节（Zhao et al, 2008）。

4.2.2 水质恶化 随着工农业发展和城镇建设的扩大，滇池周边大量工业废水和城市生活污水以及农药、化肥流入滇池。城市污水的排入大大促进了水域的富营养化，水功能基本丧失（Liu, 1997）。营养物质的丰度，尤其是氮和磷的浓度，半个多世纪以来总氮升高了近 6 倍，而总磷也升高了 1.6 倍多。高浓度的氮和磷能够对水生植物、藻类和大型

底栖动物群落产生明显的影响（Lair et al, 1998）。本文的分析也表明大型底栖动物的多样性与水体中总氮、总磷均呈负相关。武汉东湖近 20—30 年由于生活污水流入和发展养渔业的影响，底栖动物从 113 种减到 26 种，其中以毛翅目和软体动物种类的消失更甚，而霍甫水丝蚓的密度呈现快速增长的趋势（Gong, 2002）。

4.2.3　蓝藻爆发　水体超富营养化导致蓝藻的大爆发，每遇到夏季适宜的水温、充足的阳光，蓝藻等得到呈数量级疯长的最佳条件，水面便会在很短时间里出现大片“绿潮”，生态平衡遭受严重破坏。滇池水体流动性差，全年的大部分时间滇池水温都处在蓝藻适宜温度范围内。昆明充足的阳光照射、丰富的地热为滇池藻类等植物旺盛繁殖创造了良好条件（Fang, 2010）。蓝藻爆发不仅能降低水体透明度，减少光线进入，而且可以消耗水中的溶解氧，当蓝藻大量繁殖时，水中的溶解氧浓度也迅速降低，造成鱼虾、螺蛳等水生生物的死亡，底栖动物除了耐污种外很难存活。

4.2.4　水下森林消失　作为水生生态系统中的初级生产者之一——沉水植物能调节水生生态系统的物质循环速度，增加水体生物多样性，控制藻类，增强水体稳定性，从而有效提高水质（Zhao et al, 2006）。在 20 世纪 60 年代，滇池沉水植物众多，其中盖度最大的为海菜花群落、马来眼子菜群落、狐尾藻群落、蓖齿眼子菜群落和芦苇群落，占整个盖度的 70%以上（Qu & Li, 1983）。而到了 1996 年，群落结构迅速简化和退化，原来的优势物种如海菜花、轮藻等已绝迹，只剩下耐污的凤眼莲群落、喜旱莲子草群落和水葫芦群落（Yu et al, 2000）。滇池沉水植物的覆盖率从 20 世纪 50 年代的 90%下降到 2000 年的 1.8%（Gong et al, 2009）。高等水生植物为底栖动物提供了丰富的食物来源、更多的栖息地，使其生境更趋多样化，而高度的空间异质性不仅为底栖动物带来更多的摄食、繁殖和活动场所，而且更有利于躲避捕食动物的捕食、以及逃避风、水流等对其造成的危害（Newman, 1991）。因此，滇池沉水植物的消失也是底栖动物衰退的重要原因。

4.2.5　种质库的匮乏　滇池是一个相对封闭的湖泊系统，只有一条螳螂川经普渡河与金沙江连通，经过很多年的隔绝尽管形成了一些特有种，如软体动物中的螺蛳、滇池圆田螺，但由于这些年严重的污染，造成了很多特有种的灭绝，再加之进入滇池的很多河流如盘龙江、大清河等都流经昆明主城区，也遭受了严重的污染。因此，滇池四周底栖动物的种质资源库相对贫乏。而且底栖动物的自然迁移速率，特别是摇蚊科成虫一般只能在空气中生存 7 天左右，较远的种质资源库通过空气传播亦难于抵达，而水栖寡毛类（特别是仙女虫科）的迁移能力较弱。因此，滇池底栖动物的种质资源库是极其匮乏的。

从滇池无脊椎动物群落结构历史变迁这一个侧面可以看出，湖泊污染的速度越来越快，湖泊治理任重而道远。滇池污染不过 20 年的时间，可是要把它恢复到以前的样子，需要更多的时间。因此，我们要引以为鉴，每个人都要有环保意识，不能再让其他的湖泊走“先污染、后治理”的路子。

致谢：感谢中国科学院水生生物研究所滇池野外工作站在滇池采样中提供的便利，此外对滇池生态研究所潘珉提供部分滇池水体历年理化指标也深表谢意。

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附表 1　滇池大型无脊椎动物物种名录

Appendix 1　List of macroinvertebrate occurred in Dianchi Lake

		1976−1979	1982−1983	2001−2002	2009−2010
环节动物门	**Annelida**				
蛭纲	**Hirudinea**				
宽体金线蛭	*Whitmania pigra*	+	+		+
宽身舌蛭	*Glossiphonia lata*		+		
淡色舌蛭	*G. weberi*		+		
寡毛纲	**Oligochaeta**				
带丝蚓科	**Lumbsriculidae**				
夹杂带丝蚓	*Lumbriculus variegatus*			+	
仙女虫科	**Naididae**				
指鳃尾盘虫	*Dero digitata*				+
吻盲虫一种	*Pristina* sp.				+
颤蚓科	**Tubificidae**				
多毛管水蚓	*Aulodrilus pluriseta*				+
苏氏尾鳃蚓	*Branchiura sowerbyi*	+	+	+	+
坦氏泥蚓	*Ilyodrilus templetoni*				+
霍甫水丝蚓	*Limnodrilus hoffmeisteri*		+	+	+
克拉伯水丝蚓	*L. claparedianus*			+	+
巨毛水丝蚓	*L. grandisetosus*				+
奥特开水丝蚓	*L. udekemianus*		+	+	
瑞士水丝蚓	*L. helveticus*			+	
百陶溪毛蚓	*Patamothrix bedoti*				+
正颤蚓	*Tubifex tubifex*			+	+
节肢动物门	**Arthropoda**				
甲壳纲	**Crustacea**				
细足米虾	*Caridina niloticagracilipes*		+		
日本沼虾	*Macrobrachium nipponense*	+	+	+	+
秀丽白虾	*Palaemon modestus*	+	+		
中华小长臂虾	*Palaemonetes sinensis*	+	+		
昆虫纲	**Insecta**				
负子虫科	**Belostomatidae**				
负子虫	*Sphaeroderma japonicum*	+	+		+
田鳖	*Belostoma deyrollii*		+		
摇蚊科	**Chironomidae**				
羽摇蚊	*Chironomus plumosus*		+	+	+
细长摇蚊	*Ch. attenuatus*			+	+
暗黑摇蚊	*Ch. lugubris*		+		
双叉摇蚊一种	*Dicrotendipes* sp.				+
异腹腮摇蚊	*Einfeldia insolita*		+		
侧叶雕翅摇蚊	*Glypotendipes lobiferus*		+		+
小摇蚊一种	*Microchironomus* sp.				+
直突摇蚊一种	*Orthocladius* sp.				+
拟长跗摇蚊一种	*Paratanytarsus* sp.				+
花纹前突摇蚊	*Procladius choreus*			+	+

（to be continued）

（continued）

		1976−1979	1982−1983	2001−2002	2009−2010
多足摇蚊一种	*Polypedilum* sp.				+
长足摇蚊一种	*Tanypus concavus*				+
长足摇蚊一种	*T. stellatus*				+
中国长足摇蚊	*T. chinensis*			+	+
蟌科	**Coenagrionidae**				
豆娘稚虫	*Lestes* sp.		+		
划蝽科	**Corixidae**				
小风船虫	*Corixa substriata*		+		
气球虫	*Sigara sbustriata*		+		
龙虱科	**Dytiscidae**				
泽劳	*Cybister tnpunclatus*		+		
龙虱	*C.* sp.	+	+		
三点龙虱	*C. tripunctatus*	+			
黾蝽科	**Gerridae**				
水黾	*Gorris* sp.	+	+		+
鼓甲科	**Gyrinidae**				
大鼓甲	*Dineutus orientalis*		+		
水甲科	**Haliplidae**				
小头水甲	*Haliplus sauteri*		+		
水甲	*Haliplus* sp.		+		
卵形沼梭	*Haliplus ovalis*		+		
水龟虫科	**Hydrophilidae**				
水龟虫	*Hydrophilus acuminatus*	+	+		
蜻科	**Libellulidae**				
蜻蜓稚虫	*Crocothemis* sp.	+	+		
狼蛛科	**Lycosidae**				
水狼蛛	*Pirata* sp.		+		
红娘华科	**Nepidae**				
水斧	*Kanatra chinensis*		+		
红娘华	*Laccotrephes japonensis*	+	+		
蠍蝽	*Ranatra braehyusa*	+			
仰游蝽科	**Notonectidae**				
松藻虫	*Notonecta triguttata*	+	+		
溪蟹科	**Potamonidae**				
美丽拟溪蟹	*Endymion parapotamon*	+	+		
软体动物门	**Mollusca**				
瓣腮纲	**Lamellibranchia**				
蚬科	**Cobiculidae**				
河蚬	*Cobicula fluminea*	+	+		
刻蚊蚬	*C. largillierti*	+	+		
滇池蚬	*C. fenouilliana*	+			
蚌科	**Unionidae**				
背角无齿蚌	*Anodonta woodiana woodiana*	+	+		
圆背角无齿蚌	*A. woodiana pacifica*	+	+		

（to be continued）

（continued）

		1976−1979	1982−1983	2001−2002	2009−2010
椭圆背角无齿蚌	*A. woodiana elliptica*		+		
无齿蚌一种	*Anodonta* sp.	+			+
腹足纲	**Gastropoda**				
椎实螺科	**Lymnacidae**				
椭圆萝卜螺	*Radix swinhoe*		+		+
云南萝卜螺	*R. yunnanensis*	+	+		
耳萝卜螺	*R. auricularia*	+	+		
卵萝卜螺	*R. ovata*		+		
折叠萝卜螺	*R. plicatula*		+		
黑螺科	**Melaniidae**				
美丽短沟蜷	*Semisulcospira dulcis*	+	+		
粗短沟蜷	*S. iuflata*	+	+		
伏雅短沟蜷	*S. lauta*	+	+		
短沟蜷一种	*S*．sp.	+			
扁卷螺科	**Planorbidae**				
凸旋螺	*Cyraulus convexiusculus*		+		
大脐圆扁螺	*Hippeutis umbilicalis*		+		
肋蜷科	**Pleuroceridae**				
沼地螺一种	*Paludomus* sp.	+			
田螺科	**Vivparidae**				
滇池圆田螺	*Cipangopaludina dianchiensis*				+
中国圆田螺	*G. chinensis*	+	+		
中华圆田螺	*G. cathayensis*	+	+		
膨胀圆田螺	*G. ampullacea*	+	+		
球圆田螺	*G. ampulliformis*		+		
螺蛳	*Margarya melanioides*	+	+	+	+
牟氏螺蛳	*M. argarya mondi*	+	+		+
光肋螺蛳	*M. mansugi*				+
长螺蛳	*M. elongata*		+		
乳顶螺蛳	*M. tropidophora*		+		
纹沼螺	*Parafossarulus striatuaus*		+		

“+”表示出现过的物种（occured taxa）。

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甘肃定西华家岭土壤纤毛虫群落对生态恢复的响应

BACK

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摘要：为了解土壤纤毛虫群落对生态恢复下的土壤环境的响应，于 2007 年 9 月—2008 年 8 月用活体观察法和“三级十倍环式稀释法”对甘肃定西华家岭 5 个不同恢复阶段的人工云杉林和 1 个荒草坡对照点的土壤纤毛虫群落以及季节动态进行了研究，探讨了土壤纤毛虫群落组成对生态恢复下土壤环境的相关性。共鉴定到 127 种纤毛虫，隶属于 3 纲 9 目 34 科 50 属。研究发现，各不同恢复年限土样中土壤纤毛虫的物种分布存在明显差异，并随恢复时间的延长，样点间物种相似性减小，群落组成复杂化，丰度、物种数和物种多样性指数均呈上升趋势。优势类群也发生了响应，由 I 号对照样点和恢复初期 II 号样点的肾形目变为恢复后期样点的下毛目。结果显示，土壤纤毛虫群落动态很好地响应了生态恢复过程中土壤环境条件的变化。土壤纤毛虫群落可用于陆地生态恢复评价，但要建立有效可行的、具有普遍意义的评价指标体系，尚需大量的和系统的工作。

关键词：华家岭；生态恢复；土壤纤毛虫群落；生态响应；季节动态
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Response of the soil ciliate community to ecological restoration in Huajialing, Dingxi, Gansu

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Abstract: To obtain a better understanding of the responses of soil ciliate communities to ecological restoration, a quarterly survey of the soil ciliate community and seasonal dynamics across five sampling sites of artificial spruce forest was undertaken. A contrast sampling site of wild grassland was used and live observation ciliates and the three level ten-fold dilution method was used in Huajialing, Dingxi, Gansu. A total of 127 species were identified, belonging to three classes, nine orders, 34 families and 50 genera. Results show that the species distribution had obvious differences across the sampling sites, the community structure of soil tended to be complicated and species comparability decreased gradually with the number of restoration years, and abundance, species richness and species diversity index showed an upward trend. The dominant groups of soil ciliates changed during ecological restoration. Colpodida was the dominant group in sampling site I and site II, whereas Hypotrichida was the dominant group in the late recovery sampling sites. This study shows that the dynamics of the soil ciliate community better respond to soil condition changes in the ecological restoration process. Although the soil ciliate community can be used to evaluate the effect of ecological restoration of terrestrial ecosystems, plenty of further systematic research to establish an effective and feasible evaluation index system is required.

Key words: Huajialing; Ecological restoration; Soil ciliate community; Ecological response; Seasonal dynamics

针对西部生态环境持续恶化的严峻形势，我国于1999年开始实施的以退耕还林（草）为主的生态环境保护和建设工程，目前已取得了明显的生态效应和经济效益。植被类型及其发育状况决定了生态系统中其它成分的组成和结构特征，已有大量植被状况与土壤动物群落相关关系的研究 (Chen & Yin, 2000; Zhang et al, 1999; Liao et at, 1997)，证明土壤动物群落组成结构与植被状况是密切相关的。伴随

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生态恢复下植被群落的演替，土壤有机质、pH 值、有效磷、土壤含水量、水解氮等发生不同程度的改变，使得土壤理化性质不断得到改善，而这些又是影响土壤动物生长繁殖的主要环境因子 (Su et al, 1995)，故而对土壤动物的群落组成及多样性产生显著影响。目前，土壤动物对生态恢复的响应研究被很多学者所关注，但主要集中在对大型土壤动物的研究 (Adl et al, 2006; Xu et al, 2005; Xu et al, 2006)。土壤纤毛虫对生态恢复响应方面的研究尚属空白。

土壤纤毛虫作为土壤生态系统微型生物群落 (microbiota community) 的重要组成部分，在土壤生态系统的物质循环和能量流动中发挥着重要作用。由于土壤纤毛虫具有对环境变化十分敏感的特点，故可用土壤纤毛虫的环境效应参数(群落组成、丰度及多样性等)来评价、监测和预报土壤环境的变化 (Ning et al, 2007)。Petz & Foissner (1989) 研究发现农药林丹 (六氯化苯) 对土壤纤毛虫有急性致毒效应，且纤毛虫的数量和种群结构发生明显改变。Xu & Mo (2001) 对李坑垃圾填埋场垃圾渗滤液淋灌的土壤中的原生动物群落进行研究发现，即使是较低浓度的垃圾渗滤液，对土壤原生动物群落也造成了较大的伤害。Liu et al (2007) 研究了兰州市东岗地区污染土壤中原生动物后认为其物种多样性和群落组成特征可以初步评价土壤的污染状况。作者于 2007 年 9 月至 2008 年 8 月，对甘肃定西华家岭生态恢复区土壤纤毛虫群落以及土壤环境质量进行了研究，旨在了解华家岭生态恢复区土壤纤毛虫在生态恢复与未恢复生境下其群落的演替变动特征，进而为利用土壤纤毛虫评价退耕还林区生态恢复过程中土壤环境质量提供基础资料。

1 材料和方法

1.1 样区概况

甘肃定西华家岭人工云杉林恢复区——华家岭林带(35°22′54″~35°43′40″N, 104°52′48″~105°28′06″E)，地处黄土高原丘陵沟壑区，位于祁连山东部陇西旋卷构造体系内回旋褶皱带，海拔 2 000~2 586 m。华家岭属南温带半湿润－中温带干旱区气候区，年均气温 3.6~6.3℃，年降水量 350~550 mm；大气相对湿度 60%~70%，干燥度 0.8~1.2；年平均日照时数 2 500.1 h，无霜期 148 d。主要土地类型是黑垆土。

20 世纪 70 年代末，为改变人类活动对生态和环境的破坏，该地区开始人工营造“华家岭林带”，以云杉、落叶松、油松作为该区植被恢复的主要树种，进行了大规模造林。经近 30 年的努力，植被恢复已显示出一定的生态和环境效应。

1.2 样地设置和采样

所选样地位于华家岭林业站大牛试验场附近(35°22′071″~35°23′387″N,105°01′362″~105°03′657″E，海拔 2 271~2 386 m)。实验按照恢复时间的不同在定西华家岭人工云杉林生态恢复区选择了 5 个不同恢复阶段的样点，并另选 1 个人为破坏但未恢复的荒草坡样点作为对照 (图 1)，选择样点和对照区时考虑海拔、坡向和土壤类型等方面的因素以选择相似的生境。其研究区海拔、凋落物和植被情况和见表 1。

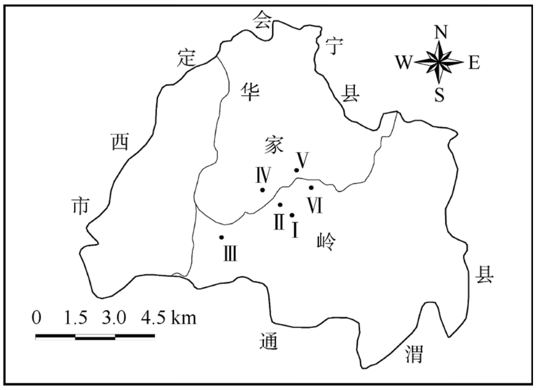

图 1 华家岭土壤纤毛虫采样点示意图

Fig. 1 Sampling sites of soil ciliates of Huajialing

Ⅰ：蛤蟆石 (对照样点) [Hamashi (contrast sampling site)]; Ⅱ：王家梁 (6 年生云杉林) [Wangjialiang (6 year-old spruce forest]; Ⅲ：小牛沟 (12 年生云杉林) [Xiaoniugou (12 year-old spruce forest)]; Ⅳ：南家屯 (17 年生云杉林) [Nanjiatun (17 year-old spruce forest) [; Ⅴ：黄家尧 (22 年生云杉林) [Huangjiayao (22 year-old spruce forest)]; Ⅵ：大牛试验场 (27 年生云杉林) [Daniushiyanchang (27 year-old spruce forest)]。图中粗线：华家岭界限; 细线：公路 (heavy line symbolized the border of Huajialing; hairline symbolized the road)。

土样采集分别于 2007 年 10 月(秋季)、2008 年 1 月(冬季)、2008 年 4 月(春季)、2008 年 7 月(夏季)的月初进行。在每个样点面积约 400 m^2 的范围内，拣去表面上的新鲜凋落物，用 15 mL 圆筒形采样器依棋盘式采样法采集 0~5 cm 土壤层的土样 25 个并进行相关记录(表 1)。剩余土样倒入白瓷盘中，纱布盖住自然风干。在此过程中，紧闭门窗并用透气草纸覆盖土样，以防止外界空气中的纤毛虫孢囊进入土样。土壤温度、含水量和 pH 测定的样品均为湿样，4℃保存备用。营养元素的测定样品为自然风干土。

表 1　各样点环境因子

Tab. 1　Environment factors in various sites

样点 Sampling sites	海拔 Altitude (m)	植被状况 Status of vegetation	凋落物 Litters (cm)	季节 Seasons	温度 Temperature (℃)	含水量 Water content (%)	有机质含量 Organic matter (%)	总氮量 Total nitrogen (%)	总磷量 Total phosphorus (%)	pH 值 pH
I 蛤蟆石 Hamashi	2 271	荒草坡，无乔木层和灌木层，草本主要有白羊草、冰草和小黄菊等，人为干扰较强，植被总盖度 10%以下。	< 1	秋	19	8.43	4.000	0.390	0.048	7.22
				冬	0	5.10	4.528	0.398	0.043	7.22
				春	10	5.24	3.690	0.389	0.046	7.21
				夏	23	12.36	4.245	0.460	0.048	7.22
II 王家梁 Wangjialiang	2 313	6 年生云杉林，云杉平均高度约为 1 m。由于放牧等人为干扰减少，草本长势良好，但种类单一，总盖度 90%以上。	< 1	秋	19	12.42	2.094	0.234	0.045	7.23
				冬	0	9.63	2.747	0.254	0.043	7.22
				春	10	9.72	2.068	0.211	0.034	7.21
				夏	23	17.03	4.330	0.387	0.039	7.21
III 小牛沟梁 Xiaoniugouliang	2 386	12 年生云杉林，云杉平均高度约为 3 m。旱生草本频度降低，出现较复杂的林下植物种类，林分已形成乔、灌、草等 3 层结构，总盖度 90%以上。	1～2	秋	17	24.49	3.888	0.391	0.037	7.21
				冬	-1	13.40	3.962	0.416	0.039	7.21
				春	9	15.05	3.962	0.381	0.036	7.21
				夏	22	23.61	4.132	0.388	0.035	7.21
IV 南家屯梁 Nanjiatunliang	2 359	17 年生云杉林，林分演化为乔灌为主的复合结构，乔木以云杉为主，平均高度约为 5 m，灌木以沙棘为主，林下草本种类较复杂，总盖度约 95%以上。	3～4	秋	18	27.34	3.956	0.406	0.040	7.22
				冬	0	14.56	4.641	0.421	0.047	7.21
				春	8.5	24.95	5.066	0.495	0.042	7.21
				夏	21.5	24.92	4.471	0.423	0.044	7.20
V 黄家尧梁 Huangjiayaoliang	2 336	22 年生云杉林，乔木层和灌木层繁茂，人为干扰基本消除，云杉平均高度 6～7 m，灌木以沙棘为主,盖度 80%以上，林下旱生草本基本退化。	4～5	秋	16	28.76	4.754	0.466	0.032	7.20
				冬	−1	16.24	5.405	0.480	0.042	7.20
				春	8	26.85	5.094	0.508	0.052	7.20
				夏	21	25.41	5.218	0.497	0.039	7.20
VI 大牛试验场 Daniushiyanchang	2 325	27 年生云杉林，乔木层和灌木层繁茂，林分密集，人为干扰基本消除，云杉平均高度约为 8 m，灌木以沙棘为主，乔、灌总盖度 90%以上，林下草本基本退化。	5～6	秋	18.5	29.07	5.349	0.481	0.048	7.19
				冬	−1	17.72	5.807	0.555	0.042	7.20
				春	8	29.17	5.525	0.512	0.050	7.21
				夏	21	27.40	5.632	0.498	0.043	7.21

1.3 土壤理化因子的测定

土温利用曲管地温计 (温度范围为：−10~60℃) 测定; 土壤 pH 值采用电位测定法, (土∶水 = 1∶2.5) 用 TSS-851 土壤湿度酸度计测定; 土壤含水量采用烘干法测定; 有机质含量采用硫酸、重铬酸钾氧化−容量法测定; 土壤全氮量采用硒粉−硫酸铜−硫酸消化法 (凯氏法) 进行消化处理, 然后在自动离子分析仪 (Quikchem) 上测定; 土壤全磷量用氢氧化钠碱熔−钼锑抗比色法测定。

1.4 定性与定量研究

定性研究采用“非淹没培养皿法”(Foissner, 1992; Foissner et al, 2002) 取每份风干土样 50 g, 分别置于直径 15 cm 的培养皿中, 25℃下培养 24 h 后即可镜检以鉴定物种。每份土样重复培养若干次, 直到未检出新见物种为止。鉴定技术包括活体观察和染色制片 (Wilbert, 1975)。物种鉴定参考文献见：Berger, 1999; Corliss, 1979; Foissner, 1987; Foissner, 1998; Foissner, 2005; Foissner et al, 2002; Kahl, 1930; Kahl, 1935; Lee et al, 1985; Lee et al, 2000; Shen & Ning, 2000。定量研究采用“三级十倍环式稀释法” (the writing group of a handbook for the research methods of soil animals, 1998) 进行纤毛虫的培养计数, 本实验采用稀释倍数 10^1~10^3。

1.5 统计分析

对鉴定到的各级分类单元及物种进行统计并划分优势类群和罕见类群, 将物种数最多的目 (order) 定义为优势类群; 次多的目定义为次优势类群; 单种的目定义为罕见类群。多样性指数依据 Margalef 多样性指数公式：$d = (S-1) / \ln N$ 计算。式中 d 为多样性指数; S 为物种数; N 为个体总数。d 值的大小表示物种多样性的高低 (Shen et al, 1990)。所有数据均用 SPSS 13.0 处理, 对环境因子和群落组成参数进行分层聚类分析; 利用物种数、丰度及物种多样性指数进行样点−季节间的无重复双因子方差分析。

2 结 果

2.1 土壤理化性质对生态恢复的响应

定西华家岭 6 个样点的土壤理化因子数据 (表 1) 表明：恢复样点的土壤含水量在四个季节均高于对照样点, 且随恢复时间的延长呈明显增长趋势; 土壤 pH 值从偏碱性降低更趋向于中性; 土壤有机质含量在恢复初期迅速下降, 6 年后其含量又不断增加, 恢复 17 年后有机质含量就高出了对照样点; 植被恢复过程中土壤总氮量、总磷量的变化与有机质含量的变化均呈先减后增趋势, 但总磷量与有机质和总氮量不同的是恢复 12 年的 III 号样点总磷量最低(四季平均值为 0.037%), I 号对照样点和恢复 27 年的 VI 号样点最高(四个季节平均值均为 0.046%), II、III、IV 和 V 号的恢复样点的总磷量均低于 I 号对照样点。

应用 SPSS 13.0 统计软件对 6 个样点中土壤理化因子的 6 个指标(含水量、土温、pH 值、有机质含量、总氮量、总磷量)进行分层聚类分析(图 2)。V、VI 和 IV 号样点在欧氏距离 1 处最先聚为一类后, 在 4 处又与 III 号样点聚为一类; I 号和 II 号样点在欧氏距离 5 处聚为一类。从 6 个样点的土壤理化因子来看, IV、V 和 VI 号样点相似性最大, III 号样点又与它们 3 个样点较为相似; I 号对照样点与 II 号样点相似性较大, 但与其他样点相似性均很低。这说明恢复时间间隔越长, 样点土壤环境之间的相似性越小。

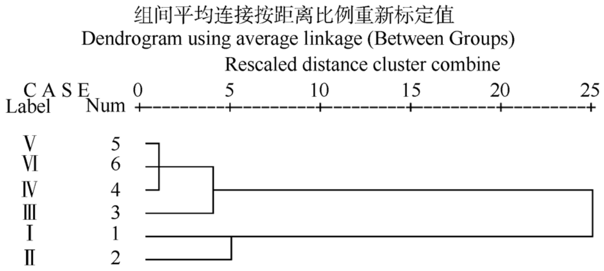

图 2 不同样点的土壤环境因子聚类分析图

Fig. 2 Dendrogram of cluster analysis on Environmental factors in various sites

2.2 土壤纤毛虫群落组成对生态恢复的响应

2.2.1 物种分布 127 种纤毛虫在各样点的分布见图 4。I 号对照样点和恢复 6 年的 II 号样点各分布有 38 种和 39 种, 分别占总物种数的 29.92%和 30.71%; III 号样点 55 种, 占 43.31%; IV 号和 V 号样点各分布有 68 种和 69 种, 分别占 53.54% 和 54.33%; 恢复 27 年的 VI 号样点物种最为丰富, 分布有 87 种, 占物种总数的 68.50%。回归分析表明, 物种数和恢复年限成良好的线性回归关系, 回归方程为 $\hat{y} = 10.029 x + 24.400$($R^2$=0.9558), 可见随着恢复时间的延长土壤纤毛虫的物种数呈增多趋势。

应用 SPSS 13.0 统计软件对 6 个样点的土壤纤毛虫物种分布进行分层聚类分析(图 3), 恢复初

期的 II 号样点与恢复中期的 III、IV 号样点最先聚为一类，再与恢复 22 年的 V 号样点汇合聚为一类，然后它们又与 I 号对照样点聚合，说明恢复期的 II、III 和 IV 号样点的土壤纤毛虫物种分布最为相似，它们与 V 号样点较相似，而与 I 和 VI 号样点物种相似性较小。可见，6 个样点的物种分布有显著差异。且随生态恢复时间的延长，样点间土壤纤毛虫物种的相似性逐渐减小。

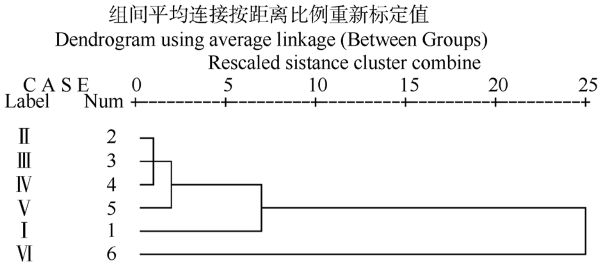

图 3　样点间土壤纤毛虫群落组成参数聚类分析
Fig. 3　Dendrogram of cluster analysis on community structure index of soil ciliates in various sites

2.2.2　群落组成　已鉴定到的 127 种纤毛虫，分别隶属于 3 纲 9 目 34 科 50 属。土壤纤毛虫群落组成见图 4，华家岭土壤纤毛虫群落组成以下毛目 (Hypotrichida) 46 种为优势类群，占纤毛虫物种总数的36.22%；肾形目 (Colpodida) 25种，占19.69%，为次优势类群；缘毛目 (Peritrichida) 只有 1 种，为罕见类群，占物种总数的 0.79%；常见类群包括：前口目(Prostomatita)、篮口目 (Nassulida)、管口目 (Cyrtophorida)、膜口目 (Hymenostomatida)、盾纤目 (Scuticociliatida) 和异毛目 (Heterotrichida)，其中以前口目种类较多，占土壤纤毛虫总数的 14.17%。

图 4 显示，I 号对照样点群落组成较为简单；II 号样点与对照样点差别不大；III~VI 号样点目、科、属和种的数目明显增加。优势类群由 I、II 号样点的肾形目逐渐演替为后期的下毛目。将未恢复的对照样点和各生态恢复阶段下的土壤纤毛虫的群落组成、物种数和优势类群做一对比总结：

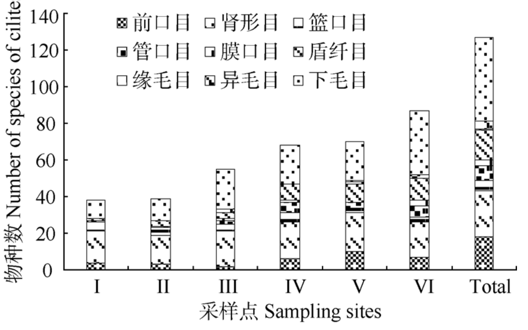

图 4　各样点土壤纤毛虫群落组成
Fig. 4　Community structure of soil ciliates in various sites

I 号未恢复对照样点分布有 3 纲 6 目 13 科 18 属 38 种。其中肾形目 (Colpodida) 17 种，占纤毛虫物种总数的 44.74%，为优势类群；下毛目 (Hypotrichida) 10 种，占 26.32%，为次优势类群；管口目 (Cyrtophorida) 和盾纤目 (Scuticociliatida) 各只有 1 种，分别占物种总数的 2.63%，为罕见类群；常见类群为前口目 (Prostomatida) 和篮口目 (Nassulida)。

恢复 6 年的 II 号样点分布有 3 纲 6 目 14 科 18 属 39 种。其中肾形目 16 种，占纤毛虫物种总数的 41.03%，为优势类群；下毛目 12 种，占 30.77%，为次优势类群；管口目仅有 1 种，占物种总数的 2.56%，为罕见类群；常见类群包括：前口目、篮口目和盾纤目。

恢复 12 年的 III 号样点分布有 3 纲 8 目 18 科 24 属 55 种。其中下毛目 22 种，占纤毛虫物种总数的 40.00%，为优势类群；肾形目 19 种，占 34.55%，为次优势类群；膜口目 (Hymenostomatida) 只有 1 种，占物种总数的 1.82%，为罕见类群；常见类群包括：前口目、篮口目、管口目、盾纤目和异毛目 (Heterotrichida)。

恢复 17 年的 IV 号样点分布有 3 纲 7 目 20 科 28 属 68 种。其中下毛目 21 种，占纤毛虫物种总数的 30.88%，为优势类群；肾形目 20 种，占 29.41%，为次优势类群；膜口目只有 1 种，占物种总数的 1.47%，为罕见类群；常见类群包括：前口目、篮口目、管口目、盾纤目和异毛目。

恢复 22 年的 V 号样点分布有 3 纲 8 目 24 科 31 属 70 种。其中下毛目和肾形目各有 21 种，分别占纤毛虫物种总数的 30%，并列为优势类群；前口目和盾纤目各有 10 种，分别占 14.29%，并列为次优势类群；缘毛目 (Peritrichida) 和异毛目各有 1 种，分别占物种总数的 0.79%，为罕见类群；常见类群包括为篮口目和管口目。

恢复 27 年的 VI 号样点分布有 3 纲 8 目 29 科 38 属 87 种。其中下毛目 35 种，占纤毛虫物种总数 40.23%，为优势类群；肾形目 19 种，占 21.84%，为次优势类群；常见类群包括：前口目、篮口目、管口目、膜口目、盾纤目和异毛目。

2.2.3 优势种 将各季度、各样点中出现频次相对较高的物种作为优势种。齿脊拟肾形虫 (*Paracolpoda steini*) 在 2007 年秋季的 4 个样点 (III、IV、V、VI)、2007 年冬季的 3 个样点 (III、IV、VI)、2008 年春季的 3 个样点 (I、II、IV) 和 2008 年夏季的 5 个样点 (I、II、III、IV、VI) 中均为优势种; 刚毛胃纤虫 (*Homalogastra setosa*) 在 2007 年秋季 5 个样点 (I、III、IV、V、VI)、2007 年冬季和 2008 年春季的 3 个样点 (IV、V、VI) 以及 2008 年夏季的 V 和 VI 号样点中均为优势种; 大口薄咽虫 (*Leptopharynx eurostoma*) 在 2007 年秋季的 4 个样点 (I、II、III、V)、2007 年冬季的 3 个样点 (I、II、V)、2008 年春季的 I 号样点和 2008 年夏季的 I 和 IV 号样点中均为优势种。由此看出, 齿脊拟肾形虫、刚毛胃纤虫和大口薄咽虫所适应的环境范围较为广泛。

从各样点优势种来看, I 号对照样点优势种种类单一, 基本都是以上分布较广的 3 种纤毛虫: 齿脊拟肾形虫、刚毛胃纤虫和大口薄咽虫, 只有在 2008 年夏季莫氏拟肾形虫 (*Paracolpoda maupasi*) 上升到优势种之列。恢复 6 年的 II 号样点以齿脊拟肾形虫、大口薄咽虫、僧帽肾形虫 (*Colpoda cucullus*) 和膨胀肾形虫 (*Colpoda inflata*) 为优势种; 恢复 12 年的 III 号样点优势种为: 齿脊拟肾形虫、刚毛胃纤虫、大口薄咽虫、膨胀肾形虫、背沟肾形虫 (*Colpoda henneguyi*) 和粗糙拟肾形虫 (*Paracolpoda aspera*); 恢复 17 年的 IV 号样点优势种为: 齿脊拟肾形虫、刚毛胃纤虫、大口薄咽虫、膨胀肾形虫、僧帽肾形虫、被发袋虫 (*Cristigera vestita*) 和伪尖毛虫 (*Oxytricha fallax*); 恢复 22 年的 V 号样点优势种为: 齿脊拟肾形虫、刚毛胃纤虫、大口薄咽虫、膨胀肾形虫、苔藓膜袋虫 (*Cyclydium muscicola*)、苔藓嗜腐虫 (*Sathrophilus muscorum*)、背沟肾形虫和莫氏拟肾形虫; 恢复 27 年的 VI 号样点优势种为: 齿脊拟肾形虫、刚毛胃纤虫、膨胀肾形虫、苔藓嗜腐虫、巴维利亚斜管虫 (*Chilodonella barvariensis*) 和苔藓游仆虫 (*Euplotes muscicola*)。

2.2.4 广布种和特有种 有 37 种纤毛虫在所有样点都出现, 为广布种, 占纤毛虫物种总数的 29.13%; 对照样点中特有种只有 1 种, 占纤毛虫物种总数的 0.79%; 恢复样点的特有种有 89 种, 占纤毛虫物种总数的 70.08%。

2.2.5 生态恢复下土壤纤毛虫物种数、丰度和物种多样性指数季节动态 从纤毛虫物种数的季节动态看(图 5), 夏季纤毛虫物种数最多, 冬季最少。其顺序为: 夏季>秋季>春季>冬季。I 号对照样点四个季节的物种数均最少, 分别为 19 (秋)、13 (冬)、18 (春) 和 21 (夏) 种; VI 号样点物种数四个季节均达到最高, 分别为 42 (秋)、38 (冬)、40 (春) 和 41 (夏) 种。

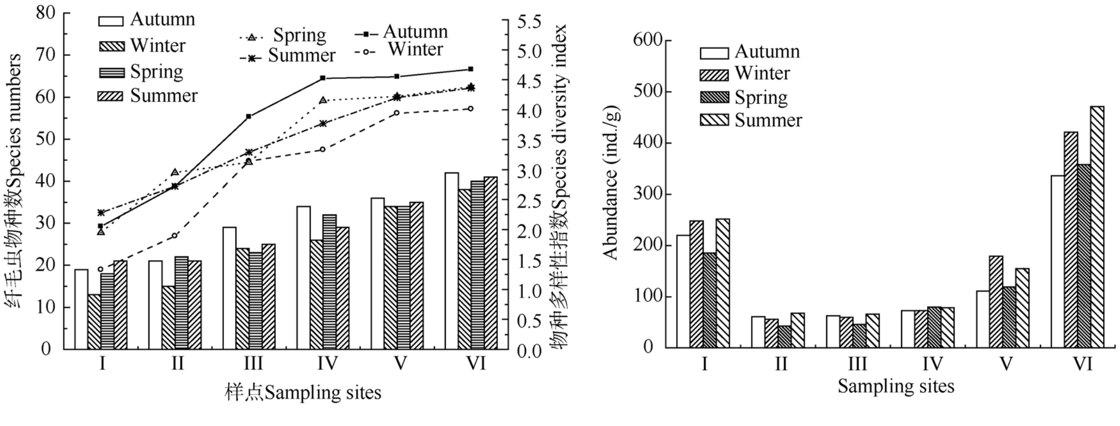

图 5 各样点的土壤纤毛虫物种数、丰度及物种多样性指数

Fig. 5 Species numbers, species diversity index and abundance of soil ciliates in various sites

土壤纤毛虫丰度的季节动态(图 5), 其 6 个样点丰度平均值由大到小的顺序为: 夏季>冬季>秋季>春季, 最高峰出现在夏季, 次高峰出现在冬季。土壤纤毛虫丰度在对照样点 I 号较高, 分别为 220 ind. /g (秋)、248 ind. /g (冬)、185 ind. /g (春)、252 ind. /g (夏); 恢复初期丰度出现了骤降, 恢复 6 年的 II 号样点丰度除夏季以外, 均最低, 分别为 61 ind. /g (秋)、56 ind. /g (冬)、43 ind. /g (春)、43 ind. /g (夏); 随着恢复时间的延长又逐渐升高, 恢复 27 年的 VI 号样点丰度最高, 分别为 336 ind. /g (秋)、421 ind./g

(冬)、358 ind. /g (春)、471 ind./g (夏)。

物种多样性指数在四个季节中, I 号对照样点多样性指数均最低, 分别为 2.05 (秋)、1.33 (冬)、1.95 (春) 和 2.28 (夏); VI 号样点多样性指数最高, 分别为 4.67 (秋)、4.01 (冬)、4.38 (春) 和 4.36 (夏)。

各样点纤毛虫群落物种数、丰度及物种多样性指数的季节变化(图 5)表明, 物种多样性指数和物种数变化一致, 随着生态恢复的年限逐渐增大, 对照样点纤毛虫的丰度除少于恢复 27 年的样点外, 都大于其他恢复期的 4 个样点, 而在生态恢复期, 纤毛虫丰度也是随着生态恢复的年限逐渐增大。利用物种数、丰度及物种多样性指数数据 SPSS13.0 进行样点–季节间的无重复双因子方差分析, 结果如下：华家岭区土壤纤毛虫物种数季节间差异极显著 ($F_{3.8}$ = 92.455, P < 0.01), 各样点间之间差异极显著 ($F_{3.8}$ = 8.586, P < 0.01); 丰度季节间差异极显著 ($F_{3.8}$ = 109.606, P < 0.01), 各样点间之间差异极显著 ($F_{3.8}$ = 4.176, P < 0.01); 物种多样性季节间差异极显著 ($F_{3.8}$ = 76.566, P < 0.01), 各样点间之间差异极显著 ($F_{3.8}$ = 12.956, P < 0.01)。

2.3 土壤纤毛虫群落结构参数与土壤理化因子的相关性

应用 SPSS 13.0 统计软件将各样点的主要环境因子 (土温、含水量、pH 值、有机质含量、总氮量、总磷量) 和纤毛虫群落结构参数 (物种数、丰度、多样性指数) 作为源变量, 进行二元变量的相关性分析(表 2)。相关性分析显示, 物种数和物种多样性指数均与含水量、有机质及总氮量呈极显著的正相关 (P < 0.01), 而与 pH 值呈极显著的负相关 (P < 0.01), 与土温和总磷量之间没有明显的相关性 (P > 0.05)。丰度与有机质含量和总氮量呈极显著的正相关 (P < 0.01), 与总磷量呈显著的正相关 (P < 0.05), 而与土温、含水量及 pH 值之间无明显的相关性 (P > 0.05)。

表 2 土壤纤毛虫群落结构参数与土壤环境因子的相关性分析(皮尔森相关性系数)

Tab. 2 Relationships between structural parameters of soil ciliates community and environmental factors of soil using Pearson's correlation coefficient

环境因子 Environment factors	物种数 Species numbers	丰度 Abundance	物种多样性指数 Species diversity index
恢复年限 Restoration stages	0.949^{**}	0.404	0.916^{**}
土温 Soil temperature	0.128	− 0.009	0.167
含水量 Water content	0.863^{*}	0.169	0.919^{**}
pH 值 pH	-0.571^{**}	− 0.106	-0.583^{**}
有机质含量 Organic matter	0.716^{**}	0.632^{**}	0.579^{**}
总氮量 Total nitrogen	0.713^{**}	0.591^{**}	0.593^{**}
总磷量 Total phosphorus	0.072	0.434^{*}	− 0.092

$^{*}P < 0.05$ 显著性水平; $^{**}P < 0.01$ 显著水平。

* Correlation is significant at the 0.05 level (2-tailed); ** Correlation is significant at the 0.01 level (2-tailed).

3 讨 论

3.1 土壤纤毛虫群落组成对生态恢复的响应

华家岭生态恢复区伴随植被的恢复通过改变土壤性质而对土壤生物群落产生影响, 其物种多样性的提高, 使群落内的其他生物协同产生相应响应。随着生态恢复年限增加, 样点的植被和覆盖度的状况发生明显改善, 地表掉落层也由恢复初期不足 1~2 cm 到恢复后期的 5~6 cm, 凋落物层的增加使土壤营养化水平提高, 并丰富了土壤纤毛虫生长繁殖所需的营养和生存条件。土壤纤毛虫群落存在明显演替, 恢复初期群落组成较为简单, 变化较小, 但伴随着土壤纤毛虫所处土壤环境的改善, 其群落组成明显趋于复杂, 对生态恢复的发生了积极响应。

土壤纤毛虫优势类群由 I、II 号样点的肾形目逐渐演替为恢复后期的下毛目。优势种种类亦逐渐增多并趋于复杂, 说明随着植被的恢复与土壤环境的改善, 有更多的纤毛虫物种适应环境并成为优势种。从优势种的分类阶元上来看, 肾形目种类最多, 这与肾形目对恶劣环境有强烈的适应性有关, 肾形目能在人为破坏严重、植被覆盖率低的土壤环境中占优势; 但是随着植被的恢复和土壤环境的改善, 下毛目所占比例逐渐增加并成为优势类群, 这是因为下毛目多为食细菌者, 植被恢复使得凋落物层加厚、土壤中腐殖质增多、细菌大量繁殖, 从而为其提供较为丰富的食物来源, 丰厚的凋落物也为其提供了丰富的趋触界面。

物种数、丰度和物种多样性指数等结构参数均能客观地反映土壤状况及其变化趋势。其中物种多样性指数可直接反映生物群落本身结构的复杂程度、稳定性大小和生态环境质量的优劣。研究区经过近 30 年的恢复, 与对照的退化生态系统相比, 5

个不同恢复阶段的人工云杉林样点土壤纤毛虫物种数和物种多样性指数均高于对照样点，且随着恢复时间的延长而升高，表明土壤纤毛虫群落更趋于复杂和稳定。物种丰度、物种多样性指数均在恢复27年的VI号样点出现高峰，并与物种数量峰值相吻合，表明该时期所设样点在所有样点纤毛虫多样性较高，土壤环境综合状况较好。由此可见，土壤纤毛虫对在生态恢复下土壤环境的改善发生响应，显示出对土壤生态系统生态恢复的指示作用。

3.2 生态恢复下土壤纤毛虫群落组成与土壤环境因子的关系

土壤纤毛虫物种数的季节动态与土温和含水量的季节动态是相一致的，在6个样点中，夏季和冬季分别是四季中土温和含水量最高与最低的季节，对应的物种数也分别是四季中最高点和最低点，故纤毛虫物种数的季节动态与土温和含水量的季节变化关系密切。此外，夏季又是四季中有机质和总氮量最高的季节，这也可能是该季节物种数最多的原因之一。I号对照样点四个季节的物种数均最少，VI号样点物种数四个季节均达到最高。Ning & Shen (1998) 研究发现土壤含水量、有机质含量和总氮量对土壤原生动物的生长发育和繁殖均有影响；Finlay et al (1986)、Beaver & Crisman (1990) 也研究发现，纤毛虫物种数随营养的增加而增加。在本研究中，I号对照样点含水量最低，物种数也最少；在II~VI号恢复样点，含水量、有机质含量和总氮量均逐渐升高，物种数亦逐渐增加。

随生态恢复，土壤纤毛虫丰度呈现剧降后，逐升的变化趋势，这与土壤总氮、总磷和有机质的含量变化均呈先减后增趋势相吻合。土壤氮主要来自有机质的分解，其含量的变化与土壤有机质的变化有着密切的关系。此外，土温也是影响土壤纤毛虫生长繁殖的重要生态因子之一。许多研究表明，在一定范围之内，土壤原生动物的丰度与温度、有机质含量和总氮量均呈正相关关系 (Opperman et al, 1989)。中国典型地带土壤原生动物丰度一年中有1个或2个高峰，大都出现在夏季 (Ning & Shen, 1998)，本实验也得到同样的结论，从4个季节的土壤理化因子来看，2008年夏季，土温、含水量、有机质含量和总氮量均达到了全年最高，因而该季度土壤纤毛虫丰度达到了最高峰；2007年冬季有机质和总氮量也较高，故丰度相应出现次高峰。此外，相关性分析发现土壤有机质含量和总氮量对土壤纤毛虫丰度影响极显著，总磷量对其影响显著，皮尔森相关性系数大小显示土壤有机质对土壤纤毛虫丰度影响比总氮大，这与 Ning & Shen (1998) 利用逐步回归分析北热带云南西双版纳的土壤原生动物丰度与有机质、总氮和总磷的关系后得出的结论相一致。

土壤纤毛虫物种数、物种多样性指数随着恢复年限呈增长趋势，这与生态恢复下有机质及总氮含量都呈极显著的正相关，说明生态恢复下，土壤环境的有机质及总氮含量是影响微食物网中群落组成稳定性的主要因素。此外，其物种数、丰度和物种多样性指数与多个环境因子存在明显的相关性，也显示出土壤纤毛虫群落对生态恢复下土壤环境的指示作用。各生态恢复样点的土壤纤毛虫群落组成间的相似性以及参数变化显示出其群落组成的演替，并且很好的响应了生态恢复下土壤环境的变化。

3.3 土壤纤毛虫在生态恢复评价中的应用

土壤纤毛虫作为土壤生态系统微型生物群落的重要组成部分，具有个体微小、现存量大、生活周期短、分布广、形态和遗传分化低、对土壤环境变化敏感性高等特点。土壤纤毛虫群落可用于陆地生态恢复评价，因而可以用土壤纤毛虫群落结构及参数来评价生态恢复效果。本研究中，随着生态恢复时间的延长和植被的恢复，一些较为敏感且不受季节影响的土壤纤毛虫，如背沟肾形虫 (*Colpoda henneguyi*)、纺锤康纤虫 (*Cohnilembus fusiformis*)、蝶形康纤虫 (*Cohnilembus vexillarius*)、有尾片尾虫 (*Urosoma caudata*)、活动恩氏虫 (*Engelmanniella mobilis*) 等在恢复初期开始出现；有些也开始适应土壤环境形成优势种。所以，这些土壤纤毛虫可以作为土壤环境生态恢复初期的指示种。此外，苔藓嗜腐虫 (*Sathrophilus muscorum*)、椭圆嗜腐虫 (*Sathrophilus ovatus*)、苔藓膜袋虫 (*Cyclydium muscicola*)、苔藓瘦尾虫 (*Uroleptus muscorum*)，尖锐尖毛虫 (*Oxytricha acuta*)、念珠角毛虫 (*Keronopsis monilata*)、苔藓游仆虫 (*Euplotes muscicola*)、近亲游仆虫 (*Euplotes affinis*) 等对土壤环境变化敏感性高且不受季节影响物种常存在于土壤含水量、土壤营养化水平较高的生态恢复后期样点中；有些适应此时的土壤环境并且形成恢复后期的优势种，故可利用这些敏感型土壤纤毛虫对生态恢复后期的土壤质量进行初步的评价和预测。

然而，与利用纤毛虫及其它水生原生动物群落

结构和功能参数评价水质相比，纤毛虫用于生态恢复效果评价的研究才刚刚起步。要建立有效可行的、具有普遍意义的评价指标体系，尚需大量的和系统的工作。

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内蒙古赛罕乌拉自然保护区狼的数量分布和食物组成

BACK

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摘要：2006 年 1 月至 2008 年 12 月，在内蒙古赛罕乌拉国家级自然保护区运用样线法和粪便分析法，对狼(*Canis lupus*)的生态分布和食物组成开展了研究。研究结果：保护区狼的数量至少 7 只，密度为(4.18±2.88)只/100 km^2，主要分布于保护区的圣山和庆云山核心区。在圣山主要活动于山脊、道路和沟谷；在庆云山主要活动于山脊。草兔 (*Lepus capensis*) 和植物在狼的食物组成中出现率最高，其食物组成在年度间存在显著差异($P<0.01$)，冬春与夏秋季节间差异不显著($P>0.05$)。

关键词：狼；种群数量；生境选择；食物构成
中图分类号：Q959.838; Q958.12 **文献标志码：**A **文章编号：**0254-5853-(2011)02-0232-04

Population, distribution and food composition of wolves (*Canis lupus*) at Saihanwula Nature Reserve, Inner Mongolia

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Abstract: To provide initial value for population restoration and management of wolves (*Canis lupus*) in the wild, line transect survey and fecal analysis method were used to study the population ecology of wolf at Saihanwula National Nature Reserve, Inner Mongolia. The results revealed that the population number was at least seven within the reserve and population density was 4.18±2.88 individual per 100 km^2. The wolf population was mainly distributed in Shengshan and Qinyunshan core areas; active sites appeared mostly along mountain ridges, roads and valleys at Shengshan and mountain ridges at Qinyunshan. Hare (*Lepus capensis*) and plants occurred frequently in the food composition of wolf scats. Food types varied between years but not seasons (Winter-Spring and Summer-Autumn).

Key words: Wolf; Population number; Habitat selection; Food composition

狼(*Canis lupus*)曾广泛分布于北美和欧亚大陆，但过度猎捕使其种群数量锐减，在许多地区一度灭绝(Musiani & Paquet, 2004)，自 1990 年以后通过再引入及有效的保护，狼在北美和欧洲的种群得到了良好恢复，但狼对家畜的危害又成为人们争论的热点(Meriggi & Lovari, 1996)。在生态系统中狼的地位较为特殊，它对有蹄类的健康发展和植物的生长都有影响(Joshua et al, 2008)。狼的主要猎物有驼鹿(*Alces alces*)(Carbyn & Kingsley, 1979)、野牛(*Bos gaurus*)(Bergman et al, 2006)、白尾鹿(*Odocoileus leucurus*)(Chavez & Gese, 2005)、驯鹿(*Rangifer tarandus*)(Kojola et al, 2004)、河狸(*Castor fiber*)(Baskin & Novoselova, 2008)等。我国青藏高原地区狼的主要猎物在青草期(相当于夏季)为草兔(*Lepus capensis*)，枯草期(相当于冬季)则为牦牛(*Bos grunniens*)(Liu & Jiang, 2003)，内蒙古达赉湖地区狼的主要食物为家畜(Yan et al, 2006)。在国内对狼的种群生态学研究还不多(Zhang et al, 1999),

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了解不同区域狼的生态特征有助于全面理解该物种在生态系统中的价值。本文对内蒙古赛罕乌拉国家级自然保护区狼的种群数量进行了调查，并从生境选择、食物组成等方面对狼的种群生态学开展了研究，为自然保护区狼的恢复与管理提供基础资料。

1　研究区域概况

内蒙古赛罕乌拉国家级自然保护区地处大兴安岭南段山地，地理坐标为东经 118°18′～118°55′，北纬 43°59′～44°27′，平均海拔 1000 m 以上，为中温带半湿润气候区，年平均气温 2℃，年平均降水量约 400 mm(Zhang et al, 2007)。该区是草原向森林、东亚阔叶林向大兴安岭寒温带针叶林过渡的地带，又是华北植物区系和兴安岭植物区系交错的地带，也是东北区、华北区、蒙新区动物区系过渡的地带(Zhang et al, 2007)。哺乳动物有马鹿(*Cervus elaphus*)、狍(*Capreolus capreolus*)、野猪(*Sus scrofa*)、猞猁(*Lynx lynx*)、豹猫(*Felis bengalensis*)、狼、赤狐(*Vulpes vulpes*)、貉(*Nyctereutes procyonoides*)、狗獾(*Meles meles*)、斑羚(*Nemorhaedus goral*)等，其中马鹿、狍、野猪、斑羚的种群数量较大(Li et al, 2005)。

保护区总面积为 100 446.1 hm^2，分为圣山、庆云山、乌兰坝 3 个核心区，圣山核心区总面积 4 766 hm^2，生境以沟谷杂木林和山地岩石灌草丛为主；庆云山核心区总面积 5 744.7 hm^2，生境以沙地沟谷山林和草原为主，外围区域开放为旅游景点；乌兰坝核心区总面积 5 829.6 hm^2，生境以河滩和沟谷杂木林为主(Li et al, 2005)。

2　方　法

2.1　样线设计

经过对保护区工作人员和当地居民的访问，了解狼的活动范围，在不同区域和不同类型栖息地确定了 20 条调查样线，其中圣山地区 11 条，在沟谷杂木林 5 条，山地灌草丛 6 条，样线平均长度 2.18 km；庆云山地区 5 条，在沟谷山林 4 条，草原 1 条，样线平均长度 2.4 km；乌兰坝地区 4 条，在河滩 3 条，沟谷杂木林 1 条，样线平均长度 3.75 km。

2.2　调查方法

调查时间从 2006 年 1 月至 2008 年 12 月进行，各条监测样线每个季节至少调查一次，冬季雪地调查时，除完成常规调查外，在每次新降雪后调查一次，根据雪地足迹基底的硬度判断足迹的新鲜程度。一般来说，基底较硬的足迹为隔夜留下的痕迹，而新鲜的足迹基底较松软。记录样线 5 m 左右观察到的动物足迹、粪便等活动痕迹，并跟踪观察动物的捕食痕迹、毛发、蹭迹等，确认动物的种类。在研究地区只有狼和猞猁两种大型食肉兽类，虽然两者的足迹大小相似，但形态差异较大，猞猁的足迹没有爪的痕迹，容易与狼的足迹进行区分，能够根据足迹链的不同方向、大小、新旧程度确定所代表的个体数。通过足迹链计数法估测狼的数量(Sutherland, 1999)。在野外调查的基础上，通过访问当地牧民了解狼的更多信息。

收集到的捕食动物粪便样品，测量长度和宽度，记录外部形态、发现地点和动物足迹特征，参照文献(Ma et al, 2001)确认是否属于狼。通过观察粪便的外观特征区分粪便的所属季节(由于夏秋季样本量较少，只分成夏秋和冬春季节做比较，夏秋：6～10 月，冬春：11 月～次年 5 月)，而后再通过粪便内容物进一步确定，如粪便中含有昆虫、植物种子、果皮、果核、果壳等，将其分为夏秋季。

用粪便内容物分析法对收集的狼粪进行分析(Mattioli et al, 2004; Gao et al, 1996)。采用频率法(frequency of occurrence)分析对猎物的选择倾向(Yan et al, 2006)。由于内容物多于一个物种的情况较多，用相对出现频率统计各类型食物的出现率，相对出现频率为一种食物在所有粪便中出现的频次与总频次的比例。用 χ^2 检验食物组成的年度和季节差异，显著性标准为 $P<0.05$。

3　结　果

3.1　种群数量

2006 年发现狼的活动痕迹(足迹、粪便、狼窝)42 处，2007 年发现 48 处，2008 年发现 28 处，排除同一区域距离较近的位点是同一只的可能，根据 Sutherland (1999)的方法估计得出 2006 年保护区狼的数量为 (7±4) 只，2007 和 2008 年狼的数量为至少 7 只，种群密度为 (4.18±2.88) 只/100 km^2。

3.2　生境选择

3 年中在圣山核心区发现狼活动痕迹 52 处，其中道路上发现 14 处(26.92%)、沟谷 14 处(26.92%)、山坡 4 处(7.69%)、山脊 20 处(30.77%)。这说明圣山核心区分布的狼在山脊和道路、沟谷活动较多，在山坡活动较少。在庆云山核心区发现狼活动痕迹

53 处, 其中道路上发现 9 处(16.98%)、沟谷 1 处(1.89%)、山坡 3 处(5.66%)、山脊 39 处(73.58%)、沙地 1 处(1.89%)。在乌兰坝核心区发现狼活动痕迹 8 处, 其中道路上发现 1 处(12.5%)、沟谷 1 处(12.5%)、草甸 2 处(25%)、山脊 4 处(50%)。这说明在庆云山、乌兰坝核心区分布的狼绝大部分在高海拔山脊活动。

3.3 年度食物组成

3 年中共采集狼粪便 76 份。草兔和植物的出现率最高, 为主要食物(表 1), 其次为啮齿类动物, 其余猎物种类在食物组成中所占比例不高。2007 年, 狼的食物组成中 (*n*=30)包括了发现的所有种类猎物, 与 2006 年相同 (*n*=18), 植物和草兔在狼的食物组成中比例最高, 啮齿类次之, 其余种类相对较少。2008 年, 狼的食物组成中 (*n*=28)比 2007 年少了爬行类和昆虫, 草兔比植物略高, 其次为啮齿类, 鸟类比之前两年相对较多。3 年内狼的食物组成存在显著差异(χ^2=18.696, *P*=0.0001)。

表 1 赛罕乌拉国家级自然保护区狼的食物组成
Tab. 1 The diet of wolves at Saihanwula National Nature Reserve

食物种类 Food types	2006 (*n*=18)		2007 (*n*=30)		2008 (*n*=28)		总计 Total (*n*=76)	
	出现次数 Occurrence times	相对频率 Relative frequency(%)	出现次数 Occurrence times	相对频率 Relative frequency(%)	出现次数 Occurrence times	相对频率 Relative frequency(%)	出现次数 Occurrence times	相对频率 Relative frequency(%)
啮齿类 Rodents	5	12.5	14	17.72	8	14.29	27	15.43
草兔 Hare	12	30	20	25.32	20	35.71	52	29.71
野猪 Wild boar	1	2.5	1	1.27	2	3.57	4	2.29
马鹿 Red deer	2	5	3	3.80	4	7.14	9	5.14
狍 Roe deer	0	0	1	1.27	1	1.79	2	1.14
家羊 Sheep	1	2.5	3	3.80	2	3.57	6	3.43
鸟类 Birds	0	0	3	3.80	6	10.71	9	5.14
爬行类 Reptiles	0	0	6	7.59	0	0	6	3.43
昆虫类 Insects	3	7.5	5	6.33	0	0	8	4.57
植物 Plants	16	40	23	29.11	13	23.21	52	29.71

3.4 季节性食物组成

在 76 份狼粪便中春夏季遗留的为 28 份, 冬春季遗留的为 48 份。夏秋季的食物组成中, 仅比所有种类少了野猪一种, 其中植物 (31.67%) 和草兔 (26.67%) 出现的相对频率最高, 其次为昆虫 (11.67%)。冬春季的食物组成中, 比所有种类少了爬行类, 其中植物和草兔出现的相对频率一样 (32.35%), 其次为啮齿类 (11.76%)。夏秋季和冬春季的食物组成不存在显著差异 (χ^2=13.333, *P*=0.272)。

4 讨论

4.1 狼的生境选择

猎物丰富度、森林覆盖率、道路密度和人为干扰是影响狼生境选择的主要因素(Peterson & Thurber , 1993; Zhang et al, 1999)。狼喜欢在人类干扰少、食物丰富、有一定隐蔽条件的环境生存 (Fuller et al, 1992), 常选择人口、道路密度较小的针叶和针阔混合林(Mladenoff et al, 1995; Thiel, 1985)。Larsen(2005)使用 GIS 模拟狼的栖息地, 发现包括森林覆盖率和公路因子的模型能很好地预测狼的栖息地。本研究中圣山核心区分布的狼主要活动于山脊、道路和沟谷, 很少在山坡活动, 这是由于圣山核心区人为活动少, 对狼几乎不造成影响。狼喜欢在食物丰富的环境生存, 山脊、道路和沟谷适合有蹄类迁移、饮水, 猎物资源比较丰富, 而且狼是保护区内的顶级食肉动物, 没有天敌, 因此其活动范围较广。庆云山核心区分布的狼绝大多数活动于山脊, 与圣山不同, 可能是因为庆云山地区旅游人数较多, 道路较多, 干扰较强, 同时该区域的地势比较平坦, 不适宜动物躲避, 狼大多时候活动在核心区深处海拔较高的环形山脉。

4.2 狼的食性

狼是机会捕食者, 猎物的可获得性和捕获的难易程度决定了狼捕食的猎物(Carbyn & Kingsley, 1979), 不同地区狼的主要猎物不尽相同。本地区狼的主要猎物为草兔、植物和啮齿类动物。草兔在狼的食物组成中占最重要的组成部分(表 1), 这应该

与保护区内草兔数量比较多有关 (Li et al, 2005)。通过我们的监测显示随着保护区管理力度的加强，狍子、马鹿、陆栖鸟类在保护区的数量逐年增加，可能是导致这些猎物在狼的食物组成中占有较高比例的因素。Mech & Frenzel(1971)分析指出，捕食动物的食物组成中出现植物，可能是在吞食猎物时带入或者来源于草食动物消化器官中尚未消化的植物。本研究在动物粪便中发现有完整叶片，植物占食物组成比率高且稳定，因此，认为狼有主动采食植物的行为，可能是为了补充纤维素，同时有利于促进不能消化成分的排出。狼只在冬春季捕食野猪，产生这种情况的原因可能是，在冬季野猪由于食物缺乏而导致体质虚弱，容易被狼捕食；野猪可以为狼提供更多的食物能量，一次捕食能够满足较长时间的食物来源。与内蒙古东部达赉湖自然保护区狼的食物中含有大量家畜相比(Yan et al, 2006; Gao et al, 1996)。本研究家畜在狼的食物组成中不占很大的比例，这是因为在核心区实行了严格的封山禁牧，捕食家畜现象仅在其他区域出现。

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高纤维食物对板齿鼠行为时间分配的影响

BACK

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摘要：食物资源或能量收支的变化会影响动物的行为模式。该研究采用高纤维饲料和标准鼠饲料分别饲喂两组板齿鼠，以红外摄像机录像第 20 天时各组板齿鼠取食、活动、休息和理毛等 4 种行为，分析了板齿鼠的昼夜节律及高纤维食物对其昼夜节律的影响。结果表明，板齿鼠的活动行为主要在夜间进行；高纤维食物对板齿鼠行为模式的影响主要表现在夜间活动、取食增多，而白天休息增多。

关键词：板齿鼠；高纤维食物；行为；时间分配
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Effects of high-fiber diet on timing of behaviors in *Bandicota indica*

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Abstract: Food resources and energy budget affect the behaviors and time budgets of animals. To clarify the effects of a high-fiber diet on greater bandicoot rat (*Bandicota indica*) behavior, we compared *B. indica* under a high-fiber diet and a standard rat diet using video monitoring. Our results show that *B. indica* are mainly active and feed at night, typical of nocturnal animals. A high-fiber diet resulted in a longer time to feed and become active at night and reduced the time spent feeding during the day. These findings suggest that food quality plays an important role in the behavioral timing of *B. indica*; this helps to understand seasonal changes in behavior demonstrated by *B. indica*.

Key words: *Bandicota indica*; High-fiber diet; Behavior; Time budget

动物各种行为在一天当中具有一定的时间分配模式，这是动物在长期进化过程中对各种内外环境因子的综合适应策略 (Rodo et al, 1992; Rodo et al, 1993; Tobler et al, 1998)。鼠类中有昼行性、夜行性和昼夜均有活动的种类，如鼹形鼠 (*Spalax ehrenbergi*)(Zuri & Terkel, 1996)、西伯利亚花鼠 (*Tamias sibiricus*)(Jin et al, 2004)、达乌尔黄鼠 (*Spermophilus dauricus*)(Cong et al, 2008)等为昼行性种类；而褐家鼠 (*Rattus norvegicus*)、小家鼠 (*Mus musculus*)、大仓鼠 (*Cricetulus triton*)(Cong et al, 2008)和黑线姬鼠 (*Apodemus agrarius*)、社鼠 (*Niviventer confucianus*) (Jiang et al, 2006)等为夜行性种类；青海田鼠 (*Microtus fuscus*)(Li et al, 2001)、东方田鼠 (*Microtus fortis*)(Hu et al, 2002)、甘肃鼢鼠 (*Myospalax cansus*)(Li et al, 2003)、布氏田鼠 (*Lasiopodomys brandtii*)(Liu et al, 2007)、莫氏田鼠 (*Microtus maximowiczii*)(Cong et al, 2008)等为昼夜均有活动的种类。昼夜活动节律存在显著的种间差异。虽然同一物种的行为时间分配模式具有一定刚性，但也会受食物可获得性改变的影响，如限食可使小家鼠 (Blank & Desjardins, 1985) 活动性显著增加，而使花栗鼠 (*Tamias minimus*)(Cormish &

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Mrosovsky, 1965) 活动性显著降低。随着季节变化、迁移扩散或人类耕作，野生农田鼠类常常面临食物质量的变化，而食物质量变化对鼠类的行为时间分配有何影响，尚缺乏相应的研究。

板齿鼠 (*Bandicota indica*) 隶属于鼠科 (Muridae) 板齿鼠属 (*Bandicota*)，主要分布于我国的广东、广西、福建、台湾、云南和贵州等地，以及东南亚地区，是热带亚热带地区重要的农田害鼠之一。板齿鼠多在夜间活动 (Zhang & Wang, 1998)，但尚无具体定量研究。板齿鼠以植食性食物为主，如水稻、甘蔗、甘薯等纤维类食物，也取食淀粉类和动物性食物 (Zhang & Wang, 1998; Feng et al, 2010)。食物质量变化对板齿鼠的昼夜节律和行为时间分配有何影响，尚无研究报道。本文通过比较板齿鼠在两种不同纤维含量食物驯化后的行为时间分配，揭示板齿鼠的昼夜活动规律及高纤维食物对其的影响，增进对板齿鼠的活动习性和行为的可塑性的了解，为野外板齿鼠调查和防治提供行为学参考依据。

1　材料方法

1.1　实验动物和饲料成分

实验用捕自广东省江门市新会地区农田中的板齿鼠，带回广州的动物饲养室内单只驯养于铁丝笼 (50 cm×35 cm×19 cm, 长×宽×高)中，以干稻谷饲喂，自由取食饮水，光周期 12 L∶12 D (6:00~18:00 为光照期，与当时自然光周期相似)，自然温度 (25~30℃)。

饲料成分：标准鼠料 (广东省医学实验动物中心生产, SCXK(粤)2008-0002)：热值 16.13 kJ/g，其中粗纤维、粗蛋白、粗脂肪和粗灰分含量分别为为 4.23%、21.60%、6.49%和 7.66%；标准兔料 (广东省医学实验动物中心生产，SCXK(粤)2008-0002)：热值 16.64 kJ/g，其中粗纤维、粗蛋白、粗脂肪和粗灰分含量分别为 12.42%、21.36%、5.17%和 8.74%。

1.2　实验方法

实验前选取健康成年非繁殖期、体重相当的板齿鼠 14 只(6♂, 8♀)，改喂低纤维含量的标准鼠料。一个月后，根据体重及性别将动物平均分为对照组 [3♂，4♀，平均体重(563.5±43.4)g]和高纤维组[(3♂，4♀，平均体重(536.5±44.6)g]。对照组依旧饲喂标准鼠料，高纤维组改喂高纤维含量的标准兔饲料，实验为期 20 d。实验过程中，对照组 1 只雄鼠状态不佳，除去不用作分析。

在实验第 19 d 时，以高清摄录系统进行昼夜 24 h 录像，夜间由摄像头自带红外灯补光录像。录像期间的光周期和温度与驯化期间一致。为减少观察者间的差异，固定观察者对录像进行观察记录，以每分钟 (min) 为一单位，记录期间的主要活动行为。行为分为取食、活动、休息和理毛等 4 种。取食，动物进行咀嚼、进食、饮水等行为；活动，动物在笼内走动、探视、抓咬等行为；休息，动物静止不动或处于睡眠状态；理毛，动物用嘴或爪梳理身体表面的动作 (Hu et al, 2002; Liu et al, 2007; Zhao et al, 2009)。

1.3　统计分析

统计分析在 SPSS 13.0 中进行。数据在分析前进行正态分布检验，雌雄各行为间无显著差异，合并分析。各行为数据昼夜间比较采用配对 *t* 检验，组间比较采用独立样本 *t* 检验，相关分析采用 Spearman's rho (2-tailed) 检验。数值皆以平均值±标准误 (Mean±SE) 呈现，$P<0.05$ 为差异显著。

2　结果与分析

2.1　板齿鼠的行为时间分配

对照组板齿鼠一天内各行为所占用时间和百分比分别为：取食, (69.67±5.67) min, 4.84 %; 活动, (214.17±31.87)min, 14.87%; 休息, (976.33±45.09)min, 67.80 %; 理毛, (179.83±28.41)min, 12.49%(图 1)。对照组板齿鼠夜间活动时间，占全天活动时间的 70.66 %，夜间理毛时间，占全天理毛时间的 64.32 %，显著多于白昼；夜间休息时间，占全天休息时间的 42.73 %，显著少于白昼；夜间取食时间，占全天取食时间的 51.44%，与白昼无差异(表 1)。

高纤维组板齿鼠一天内各行为所占用时间和百分比分别为：取食, (74.14±12.85) min, 5.15 %; 活动，(313.71±57.09) min, 21.79 %; 休息，(882.57±50.93) min, 61.29 %; 理毛，(169.57±14.49) min, 11.78 %(图 2)。各行为在一天中占比大小依次为休息、活动、理毛和取食，与对照组相似。高纤维组板齿鼠夜间活动时间，占全天活动时间的 77.96 %，夜间取食时间，占全天取食时间的 80.16 %，显著多于白昼；夜间休息时间，占全天休息时间的 36.08 %，显著少于白昼；夜间理毛时间，占全天理毛时间的 57.54 %，与白昼相似(表 1、图 2)。

此外，虽然高纤维组板齿鼠的各行为的日时间

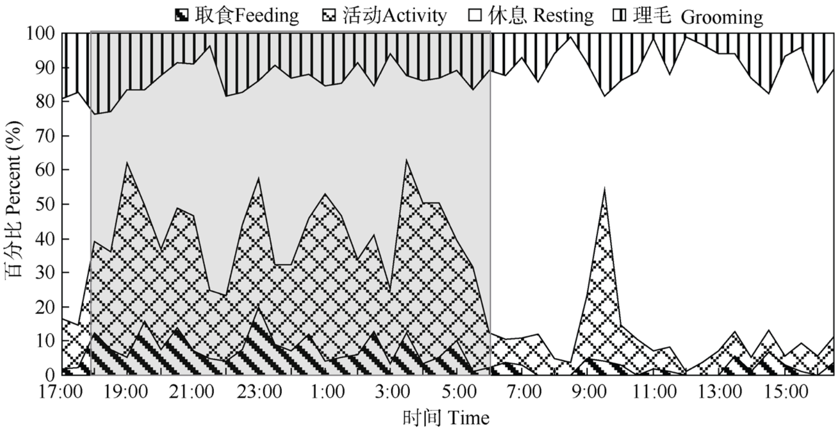

图 1 对照组板齿鼠各行为昼夜时间分配

Fig. 1 Time budget of behaviors in the control group of *Bandicota indica*

以每 30 min 内对照组 6 只实验鼠的各行为时间的均值作图, 图中灰色阴影示 18:00—6:00 的夜间时段。

Drawing with the mean time of 30 min of various behaviors in each group with 6 mice, the gray shadows shows the night time from 18: 00 to 6: 00.

表 1 对照组和高纤维组板齿鼠昼夜间行为差异的比较

Tab. 1 Comparison of Diurnal behaviors between the control group and the treatment *Bandicota indica*

		对照组 Control(min)			高纤维组 Treatment(min)			*t*	*P*
		N = 6			*N* = 7				
取食 Feeding	昼 Day	33.83	±	4.13	14.71	±	5.92	**2.560**	**0.027**
	夜 Night	35.83	±	6.97	59.43	±	9.27	−1.976	0.074
		(*t*=−0.201, *P*=0.849)			**(*t*=−5.104, *P*=0.002)**				
活动 Activity	昼 Day	62.83	±	9.84	69.14	±	7.37	−0.522	0.612
	夜 Night	151.33	±	30.83	244.57	±	53.39	−1.444	0.177
		(*t*=−2.695, *P*=0.043)			**(*t*=−3.474, *P*=0.013)**				
休息 Resting	昼 Day	559.17	±	10.31	564.14	±	11.47	−0.318	0.757
	夜 Night	417.17	±	48.37	318.43	±	51.30	1.385	0.194
		(*t*=2.656, *P*=0.045)			**(*t*=4.537, *P*=0.004)**				
理毛 Grooming	昼 Day	64.17	±	7.97	72.00	±	6.00	−0.799	0.441
	夜 Night	115.67	±	23.05	97.57	±	10.10	0.759	0.464
		(*t*=−2.632, *P*=0.046)			**(*t*=−3.148, *P*=0.020)**				

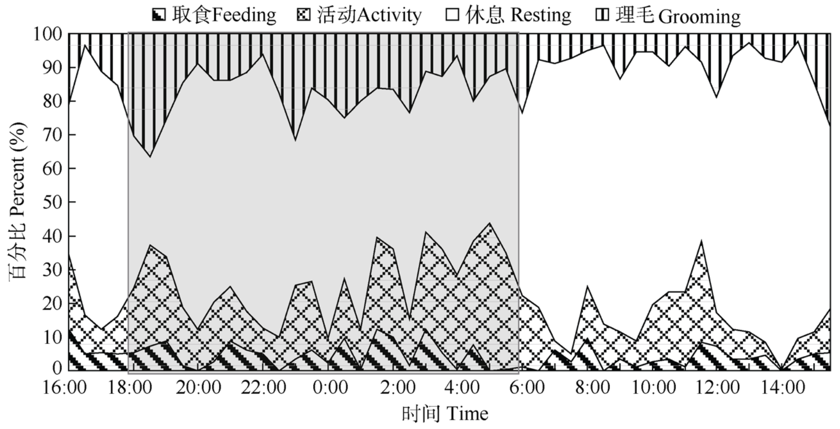

图 2 高纤维组板齿鼠各行为昼夜时间分配

Fig. 2 Time budget of behaviors in the control group of *Bandicota indica*

以每 30 min 内高纤维组 7 只实验鼠的各行为时间的均值作图, 图中灰色阴影示 18:00—6:00 的夜间时段。

Drawing with the mean time of 30 min of various behaviors in each group with 7 mice, the gray shadows shows the night time from 18: 00 to 6: 00.

分配与对照组无差异，但高纤维组板齿鼠白昼取食时间显著少于对照组，仅为对照组的 43.48 %，而夜间的取食时间比对照组增加 65.87 %(表 1)。

2.2 各行为间的相关性

对照组：休息和取食、活动、理毛都呈极显著的负相关关系(r = −0.669、−0.840 和−0.724, P<0.001)；而活动与取食(r =0.270, P<0.001)、理毛之间(r = 0.198, P<0.001)存在显著的正相关关系；取食与理毛没有显著相关性(r =0.049, P=0.369)。

高纤维组：休息和取食、活动、理毛都呈显著负相关关系(r = −0.620、−0.887 和−0.675, P<0.001)；活动与取食、活动与理毛和取食与理毛之间呈正相关关系，相关系数分别为(r =0.511、0.383 和 0.257, P<0.001)。

3 讨 论

3.1 昼夜节律

本研究表明，板齿鼠的活动行为主要在夜间进行，夜间活动占总活动量的 70 %以上；夜间的理毛行为也多于白昼；而白昼，则以休息为主。因此，板齿鼠是夜行性为主的动物。这与前人的野外观察结果一致 (Zhang & Wang, 1998)。板齿鼠作为一种生活于热带亚热带的植食性小型哺乳动物，夜行性可能是其躲避白昼的酷热和天敌的一种行为适应对策。板齿鼠的摄食行为在对照组无显著昼夜差异；而在高纤维组就表现出显著的夜行性，暗示不同环境条件下板齿鼠行为节律的可塑性。此外，板齿鼠有较多的自身理毛行为，如对照组板齿鼠的理毛行为，占总时间 12.49 %，高纤维组，占 11.78 %。自身理毛行为在非人类灵长类、鼠类等动物中发生较普遍，主要功能是保持体表卫生，也有修饰和吸引异性等作用 (Yanase et al, 1991; Imaizumi et al, 2000; Serafim & Filicio, 2002; Lv & Li, 2006)。

3.2 食物质量对行为时间分配的影响

动物的行为与动物的能量代谢需求变化有直接关系 (Halle & Stenseth, 2000)，而能量收支的变化取决于食物的能量高低和多少 (Veloso & Bozinovic, 1993)。本研究中，高纤维食物对板齿鼠行为的时间分配有一定影响，主要表现为减少白昼取食时间，更倾向于夜间取食，夜间活动行为也有一定程度增加，但未达到显著水平，对休息和理毛的影响不显著。Bondrup-nielsen (1992)给草原田鼠(*Microtus pennsylvanicus*)从出生至 6 周内饲喂低蛋白食物，结果发现饲喂低蛋白食物会使草原田鼠活动性增多。在小鼠和黑线仓鼠(*Cricetulus barabensis*)的随机饥饿期间，其活动行为也会增加 (Zhao & Cao, 2009; Zhao et al, 2009)。因此，增加活动可能是动物试图通过增加觅食以满足能量需求的一种积极的行为对策。此外，饲喂高纤维饲料的板齿鼠主要在夜间增加活动和取食，这与前人野外观察相似，板齿鼠在食物紧缺、植物枯萎隐蔽条件差的冬春季，会更多地在夜间活动觅食 (Zhang & Wang, 1998)，这可能与其较高的警觉性有关，夜间便于其隐藏，保证觅食安全。理毛行为的变化主要与食物成分、清理身体、天气因素等有关 (Perez & Vea Baro, 1999; Li et al, 2002; Hou et al, 2002)。在本研究中，高纤维组和对照组之间的理毛行为无显著差异，表明理毛行为在板齿鼠中具有一定的必要性。此外，也可能与理毛行为本身耗能较少有关。

板齿鼠是一种独居性的农业害鼠，常年在野外活动，食物质量仅是影响其行为时间分配的环境因素之一，而诸如天敌、温度、同种或共域分布的其他鼠种等对其行为时间分配的影响值得进一步的研究，这对全面掌握板齿鼠在野外环境中的行为模式，为农业害鼠防控提供有效的建议和指导都具有重要意义。

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