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Reversed sexual dimorphism in tawny owls, *Strix aluco*, correlates with duty division in breeding effort

Peter Sunde, Mikkel S. Bølstad and Julie D. Møller

Even though most bird species with a raptorial feeding habit express varying extents of reversed sexual dimorphism (RSD: females bigger than males), the evolutionary basis for its maintenance, as well as its possible secondary consequences for the ecological adaptations of the different sexes, is debated. We studied pairs of tawny owls, *Strix aluco* (females 20% heavier than males), throughout the year by telemetry to test whether any inter-sexual differences in movement patterns, resource partitioning and breeding effort correlated with RSD. Females were larger than males in all body size measures and were 16% heavier than would be expected from the difference in wing length alone. In accordance with predictions from flight economics, males moved longer distances per time unit than females, in particular during the post-fledging season, when they also fed chicks more often than the females. Males had larger home ranges than females during the post-fledging period, whereas the sexes had home ranges of equal size during the non-breeding season. Until 10 days after fledging, females foraged much closer to the offspring than males, apparently balancing their distance to offspring between the needs of offspring guarding and foraging. In males, the parent–offspring distance only increased with decreasing brood condition. The sexes did not differ in habitat use or feeding habits, rendering no indications of food niche partitioning. The study provides further evidence that selection for males to be light and energetically efficient foragers is the main evolutionary force behind RSD in raptorial birds, even when the prey base is confined by territoriality.

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Most terrestrial raptors in the orders Falconiformes and Strigiformes express reversed sexual size dimorphism (RSD: females being larger than males). As the magnitude of the RSD of different raptorial species is positively correlated with the agility and relative size of their prey, the selective basis for RSD appears somehow to be linked to feeding ecology (Newton 1979). Three general groups of mechanisms may cause and maintain sexual dimorphism in animals: (1) sexual selection, (2) inter-sexual food competition and (3) reproductive role division (Hedrick and Temeles 1989). The first option can probably be ruled out as the ultimate

cause, as sexual selection does not seems to explain the link between RSD and feeding biology across taxa (Newton 1979, Norberg 1987, Andersson 1994). Of the remaining two main sets of hypotheses, the inter-sexual food competition hypotheses (Newton 1979, Temeles 1985) share the theory that the inter-sexual size difference enables the pair to exploit a wider size range of prey resources thereby avoiding competition between the mates. In particular, this should be of importance when the pair's shared foraging range is confined, e.g. due to territoriality. Food competition does not explain the direction of the dimorphism, but may enlarge an

already existing size-difference originally caused by other factors. It has also been argued that RSD may enable males to forage in denser tree vegetation than females, due to better manoeuvrability, resulting in prey segregation on a spatial scale (Selander 1966, Earhart and Johnson 1970). Hence, some studies have found raptor females to utilize more open habitats than males (Marquiss and Newton 1981, Solis and Guttiérrez 1990), whereas others have found no differences in habitat use even in strongly dimorphic species (Kenward 1982, Widén 1989). As a secondary mechanism, large, dominant females displacing males from the best foraging habitats has been shown to produce differential habitat use in wintering hen harriers (*Circus cyaneus*) (Temeles 1986).

The reproductive role division hypotheses argue that duty division in the breeding period has resulted in selection for males being smaller or females larger than optimal for survival purposes during the non-breeding period. The advantages of small male size ("small male hypothesis") during reproduction should be better flight economy and a generally lower metabolism due to lower body weight (Earhart and Johnson 1970, Reynolds 1972, Andersson and Norberg 1981). Additionally, the increased agility of males due to smaller size and weight load should possibly increase their hunting success. One possible advantage of a larger female size is an increased ability to store extra energy as a buffer for periods during incubation when the male fails to provide food (Lundberg 1986).

In the last decade, a number of studies on the reproductive performance of Eurasian kestrels (*Falco tinnunculus*) (Hakkarainen et al. 1996, Wiehn and Korpimäki 1997, Massemin et al. 2000) and Tengmalm's owls (*Aegolius funereus*) (Hakkarainen and Korpimäki 1991, 1993, 1995) have provided support for the validity of the reproductive role division hypotheses, in particular the small male hypothesis, in these two species of semi-nomadic vole predators. However, the acceptance of the small male hypothesis, if generally applicable to all raptorial birds, does not necessarily reject the possibility that resource segregation also may form a selective basis for RSD maintenance, at least in some species. Alternatively, RSD maintained by reproductive role division may secondarily cause sex-specific resource segregation. Hence, in order to pinpoint the causal relationships behind sexual dimorphism it is necessary to comprehensively study all aspects of sex-specific differences in the ecology in a given species throughout its annual routine. The tawny owl (*Strix aluco*) should form a suitable model to examine the "niche segregation" hypothesis and the "reproductive role division" hypothesis as this owl is intermediately dimorphic (females are 15–25% heavier than males) and has a generalist feeding habit based on small mammals and birds with the pairs being residential on small, vigorously defended territories throughout the

year (Mikkola 1983, Cramp 1985). As the amount of resources tawny owl pairs are able to invest in reproduction appears to be limited by the size of the territory (Southern 1970, Hirons 1985b, Redpath 1995), food niche segregation should thus be advantageous if achievable. Even though most breeding failures occur during the incubation phases when the female relies entirely on food provided by the male (Southern 1970, Hirons 1985a), chicks may starve throughout the post-fledging season (Petty and Thirgood 1989, Coles and Petty 1997, Sunde 2001), i.e. after the females' incubation duties has been completed.

In the following, we quantify patterns of sex-differentiation in morphology, ecology and behaviour with special reference to differences between the breeding and the non-breeding seasons. By using breeding pairs as sampling units, we minimise the effects of variable environmental conditions as much as is practically possible under natural conditions. If RSD is maintained by food partitioning selection or if other factors secondarily cause a diet difference due to different optimum prey size or prey type for males and females, we would expect this difference in prey size or prey type to be measurable in a sample of adequate size. Likewise, if RSD causes differential habitat use, we should expect males to use denser tree stands more often than their mates. On the other hand, if RSD is maintained as a consequence of differential breeding effort, we should expect a clear duty division of the sexes to be found throughout the breeding season, also after the female's primary duties of incubating eggs and nestlings are completed. Accordingly, all male–female comparisons from the breeding period will be from the time after the female has finished the incubation and is free to allocate her efforts in the same way as the male.

Even though caution is required when drawing causal conclusions on the basis of comparative approaches, absence of correlations between RSD and potential ecological factors can be used to rule these out as selective forces as opposed to those that correlate strongly with RSD.

Study area, materials and methods

Tawny owl pairs were surveyed by means of telemetry during April 1998–September 2000 in the Gribskov Forest and Strødam Scientific Reserve (55° 57′ N, 12° 16′ E), 30 km north of Copenhagen, Denmark. The number and dispersion of tawny owl territories were stable throughout the period with a mean density of 1.4 pairs per km^2. The territories were vigorously defended, overlapping only in their peripheries and had constant boarders among seasons and years (Sunde 2001). As the woods were saturated with artificial nest boxes and natural tree cavities, it is unlikely that the number of

breeding pairs were limited by other factors than density dependence (Southern 1970). The data is based on nine pairs with both mates being surveyed throughout the same period and one male and two females with un-tagged mates. All pairs inhabited territories comprising continuous forest, primarily planted tree stands (age up to > 150 years) with beech (*Fagus silvaticus*), oak (*Quercus robur*), birch (*Betula pendula*) and Norway spruce (*Picea abies*) as the dominant tree species. The single male with an untagged mate and four of the nine pairs had access to continuous (3–20 ha) stands of unmanaged, pristine-like broadleaf forest with naturally decaying trees. All pairs also had access to patches of open habitats like grazed meadows, thinned tree stands, cultivated fields, gardens and fens. This habitat composition with continuous, mature forest interspersed with patches of open areas and woodland is probably close to the initial forest structure (Fritzbøger 1994) in which the natural selection processes of tawny owls has taken place during the past millennium in Denmark.

Catching, measuring and radio tagging

Adult tawny owls were netted at daytime in nest boxes or natural cavities; by night they were caught in swing door traps when bringing food to the nest box or in mist nets when attracted to hoots from a loudspeaker. The owls were weighed with a Pesola™ spring balance with a precision of ± 2.5 g. The body condition was scored on an index from 0 to 4 based on the amount of subcutaneous fat on the breast, belly and ribs, which could readily be assessed from skin colouration and texture (0 = starved: no fat, atrophied muscles, 1 = lean: no fat, no muscle atrophy; 2 = moderate: a thin fat rim along the carina; 3 = well fed: considerable areas of the breast and belly covered by fat deposits; 4 = fat: the belly covered by a thick fat layer). Body length and wing length were measured to nearest mm. Wingspan and wing areas were measured following Pennycuick (1999). The diameter of the claw on the hind toe was measured at the base with a slide gauge to the nearest 0.1 mm. The radio-tagged owls were easily sexed on the basis of their breeding duties (presence/absence of brood patch and incubating behaviour) or voice. In addition, a sample of adult owls caught and measured in the area during August–December 2000 without being radio tagged were sexed by means of molecular techniques by K. B. Desfor. The owls were supplied with an 8–13 g (including harness) backpack radio transmitter (Biotrack, Wareham, UK) mounted to the body beneath the plumage with 6 mm teflon ribbon. The radio tags transmitted for 10–12 months. Until June 2000, tags approaching exhaustion were replaced

whenever a bird was caught. After this date, exhausted radios of recaptured owls were removed.

Calculations of energy expenditure of flight and manoeuvrability

Based on the data on wingspan, wing area and body mass of the birds, the energy costs and manoeuvrability of flapping and gliding flight were calculated (Pennycuick 1989) using the computer program "flight.bas" (courtesy of C.F Pennycuick). Since no significant intra-sexual correlations between wing length and mass were found in our data (see later), the calculations were based on mean values for wingspan and wing area for each sex.

Division of time periods

In the following, we divide the annual routine into a nesting period (from egg laying through fledging, about 2 months), post-fledging period (from fledging to independence of offspring 55–83 d later) and a non-breeding season. We sub-divide the nesting period into an incubation phase (day 0–40 from incubation start) and a nestling phase (from day 41 after incubation start, when the oldest chicks were 5–10 d old, until fledging). Likewise, the post-fledging period is sub-divided into 3 intervals (days 0–10, 11–45 and 46–independence). The date of incubation start was found by backdating the brood from the age of the oldest chick assuming 30 d of incubation (Cramp 1985). We defined the post-fledging period as having ended when the young no longer begged for food at night (checked every 1–2 nights).

Telemetry routines

In the following, we distinguish between observations made during the day when the owls were roosting and "night" observations made when the owls were active. Daytime data were collected as spot observations, i.e. the owls were homed at their roosts and their distance to family members were noted. Night data were primarily based on spot observations, obtained by triangulation usually at distance of 20–50 m. Throughout the year, two to four night positions were obtained per owl per week, usually one per night.

In order to gather detailed information about the movements of the owls, food-provisioning rates, etc. the active owls were surveyed for 3-hour periods (10 p.m.–1 a.m.) during which every detectable (≥ 30–40 m) movement was registered. By summing the distances between the telemetry fixes, a minimum

displacement distance over time (MDD) was calculated for the total period. As not all movements were detectable, MDD is an underestimate of the true displacement over time. However, the owls usually perched long enough ($>3-5$ min) to permit a reliable record of location; the underestimation error is unbiased with respect to sex as long as the sexes show similar patterns of movement. To ensure homogeneous environmental conditions, the surveys were only performed at nights with no or negligible rain and wind speeds of ≤ 3 (gentle breeze) on Beaufort's scale. Mates were surveyed on consecutive nights, yielding a matched pair of observations. To ensure that the movements of the females were not confined by the need to protect vulnerable young, matched-pair surveys during the breeding season were not done until one week after the owlets had fledged and were out of the reach of foxes. A maximum two paired surveys were conducted on the same pair during the post-fledging season a minimum of four weeks apart. In the data from the non-breeding season, a pair was represented with maximum of three paired surveys, two months apart (minimum).

Statistical analysis of home range and movement data

Range size was measured as 95% fixed kernels (Worton 1989) with ad hoc estimation of the smoothing parameter, using the Animal Movement extension version 2.2 for ArcView (Hooge and Eichenlaub 1997). In order to secure comparable environmental conditions in the post-fledging and non-breeding period, we used only spatial data for May–October for the home range calculation. Since re-sampling analyses led to stable kernel home range estimates if based on ≥ 18 fixes, we accepted 18 telemetry fixes as the smallest sample size allowing for a kernel home range to be calculated. In two owl samples originally represented by $15-17$ telemetry fixes, additional fixes were added by selecting some from the 3-hour surveys taken at regular intervals (every 60 or 90 min). Even though these fixes were not entirely independent when tested in an autocorrelation analysis, they do not bias the estimate as long as they were sampled with a regular time interval (De Solla et al. 1999).

In order to achieve normally distributed data and variance homogeneity, MDD was square root transformed prior to the analyses. In order to obtain as much information as possible about differences in MDD between breeding phases and/or sexes within a pair, all MDD-data from the post-fledging or non-breeding period were analysed in a 3-way ANOVA (sex, phase, pair ID), correcting for possible inter-pair differences by entering each pair as a random factor. In a more rigorous test, we used only paired MDD-data tested by Wilcoxon's matched pair signed rank test.

Distance to young offspring: guarding vs foraging

As the tawny owl guards its young offspring against predators (Wallin 1987), we used the parent–offspring distance (POD) as an index of a brood defence effort as opposed to foraging (night, occasionally day) or selection of safe roosts (day). To test for variation between the sexes and phases of the breeding seasons, we used the mean POD for each individual (MPOD) with ≥ 2 observations from a given phase. In those cases where data on an owl existed from more than one breeding season, MPOD-data was pooled. To obtain normality and variance homogeneity, the values were log transformed prior to the analyses. The overall differences in MPOD among the sexes and the breeding phases were tested with repeated measures ANOVA.

To test whether the owls regulated their breeding effort between offspring guarding and foraging, we correlated MPOD during the late nesting phase and early post-fledging phase against the brood condition score determined on the basis of the condition of the poorest chick in the brood ($1 =$ starvation mortality recorded in the brood later in the breeding cycle; $2 =$ lean chick: no subcutaneous fat, atrophic muscles, continuous noisy begging cries in the nights after fledging; $3 =$ moderately good condition: fewer begging food cries during night; $4 =$ well fed: few/no food cries during the nights after fledging). The condition of the poorest chick was selected as index since it was the poorest chicks in the brood that would be the first to die of starvation-related death causes.

Since we found MPOD at night to increase with decreasing brood condition around fledging (see below), we tested the effects of chick age (in days from fledging), chick vulnerability (the altitude of the lowest chick in the brood) and chick condition on the POD from day $0-20$ after fledging. In this analysis, we used each night location as an observation unit, correcting for inter-pair differences by entering the pairs as a random factor in the ANCOVA model. In a subsequent ANCOVA model, which also incorporated the effect of brood hungriness, the pair-effect was excluded, as it confounded with the condition of the brood.

Habitat use of foraging owls

In order to test whether sex-specific differences in flight performance resulted in differential usage of habitats with different canopy density, the type of habitats used were obtained for telemetry fixes with a measurement error of ≤ 15 m, using a Geographic Information System (ArcView 3.2 and Arc Info 8.0, ESRI).

Habitats were categorised according to vegetation closure (mapped and digitised by us) as follows: 1: open land, 2: open tree vegetation, 3: moderately dense tree vegetation, 4: closed vegetation and 5: very closed

vegetation. All data available for each individual were used except for that of females from the nestling period and first 10 d of the post-fledging period while their movements were confined by the offspring. Differential use of the different habitat categories (proportional use of male vs proportional use of female) was tested with compositional analysis (Aebischer et al. 1993). In the compositional analysis, the density categories 1–2 and 4–5 were pooled due to few observations in the most extreme categories. As an alternative test, the mean score of the canopy closure categories utilised by the mates was tested by means of a paired t-test.

Diet composition

Information about the diet composition of the individual birds was obtained from pellets from pairs where the mates used separate roosts during the same period. For each individual owl, the diet composition was estimated by summing the minimum number of prey items recorded in each sample of pellets, i.e. by taking the number of the most numerous skeletal or cuticular (invertebrates) parts (e.g. number of left lower mandibles in animals and upper beak in birds). Almost all mammals could be determined to species and their weights were estimated from our own trap data or from handbooks (Niethammer and Krapp 1978–1990). Bird remains were classified as tit/warbler size: 15 g, finch size: 21g, thrush size: 95 g and magpie size: 200 g. Anurans were categorised as small (5 g), medium (15 g) and large (40 g).

Overall sex differences in diet were tested as (1) composition of prey types (categorised as ground-living mammals, birds/bats and amphibians/invertebrates) and (2) size (vertebrate prey only). Differences in prey composition were first tested using the prey items as statistical units as the significance of the partial sex-by-prey type association in a saturated log-linear model including the effects of sex, pair and prey type (Norusis 1994). As a highly significant individual difference in

diet composition was found (see below), casting doubt on the assumption of independence of the observations within each individual, difference in diet composition based on biomass was also tested by compositional analysis. The difference in mean and median vertebrate prey size was tested with paired t-tests. Due to the limited number of data available we were unable to split the analysis into seasons or breeding stages.

Results

Morphometric measures

On average, females were larger than males in all measured characters (Table 1). The dimorphism was highest in the diameter of the hind claw and smallest in the lengths of the wing and body (Table 1). Throughout the year, the dimorphism in body weights appeared to be higher than would be predicted from the difference in wing or body length, though both sexes were significantly heavier in winter than during the summer (Table 1; two-way ANOVA on the 1st measure of 12 males and 21 females: sex: $F_{1,28} = 34.07$, $p < 0.0001$; period: $F_{3,28} = 4.815$, $p = 0.008$; not significant and excluded from the model: sex × period: $F_{3,25} = 0.623$, $p = 0.61$). Since the body weight was heavily dependent on the fat loads (Fig. 1), it was therefore necessary to correct for the condition score while calculating the dimorphism in body size. In an ANCOVA model, there was a highly significant, additive effect of sex on body weight even after having accounted for the effects of wing length and condition (Table 2). Hence, a female would, on average, be 16% heavier than a male with the same wing length and condition score. In contrast, body weight did not correlate significantly with wing length when accounting for the effect of condition score and sex (Table 2).

From the lightest male (392 g) to the heaviest female (659 g), there was an estimated 126% increase in the minimum energy expenditure of flapping flight (Fig.

Table 1. Morphometric measures of adult tawny owls caught in the study area 1998–2000. The dimorphism index is defined as $DI = 2[\bar{x}_F - \bar{x}_M]/[\bar{x}_F + \bar{x}_M]$, where $\bar{x}$ is the one-dimensional transformation of the measure of interest, (i.e. the square root of mean wing area and cube root of mean body weight). The weight figures are based on one measure per owl per time phase.

|	Males			Females			t	P	DI (%)
	$\bar{x}$	SD	n	$\bar{x}$	SD	n			
Wing length (mm)	267	7	12	273	7	21	−2.540	0.016	2.4
Wingspan (mm)	897	17	9	919	22	12	−2.479	0.023	2.4
Wing area (cm²)	1511	81	9	1624	110	12	−2.600	0.018	3.6
Body length (mm)	367	10	11	377	15	18	−2.042	0.050	2.8
Hind claw diameter (mm)	3.7	0.5	8	4.2	0.4	13	−2.990	0.008	12.8
Body weights									
-Incubation period (day 0–40)	431	55	2	575	56	9	−3.234	0.012	9.6
-Nestling/fledging period	417	20	6	515	47	9	−4.767	0.0003	7.0
-Non-breeders, May–Oct	441	26	4	502	25	7	−4.075	0.003	4.3
-Non-breeders, Nov–Feb	471	42	7	567	58	9	−3.665	0.003	6.2
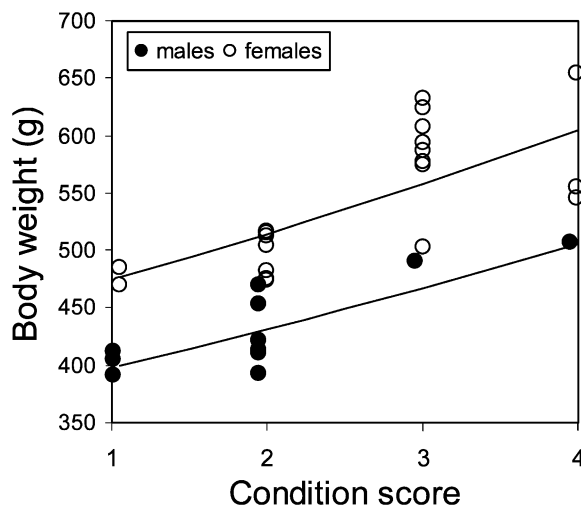
Fig. 1. Body weights of 12 male and 22 female tawny owls plotted against body condition (1 = lean, 2 = moderate, 3 = well fed, 4 = fat). The upper and lower lines represent the predicted body weights of females and males with average wing length (Table 2) as a function of condition score.

2A), a 26% increase in minimum gliding speed (Fig. 2B) and a 58% increase in circling radius (Fig. 2C). In individuals optimising their flight performance by minimising their fat loads, the differences between a male and a female of average size (based on data from Table 1 and the body mass equation in Table 2: males, 398 g, females, 475 g for fat score = 1) would be 29% in minimum energy expenditure of flapping flight (19.7 vs 25.5 W), 5.5% in stalling speed (5.1 vs 5.4 m/s) and 11.1% in circling radius (7.5 vs 8.3 m).

Movement patterns and food provisioning rate

In both sexes, the MDD was higher during the post-fledging period than during the non-breeding period (Fig. 3 and 4, Table 3). During both periods, males moved considerably more than females, but the relative inter-sexual difference in MDD was highest during the post-fledging period (Fig. 3, Table 3). The MDD of males during the nesting phase tended to be lower than during the post-fledging period (Fig. 3; $t_{20} = 1.942$, $p = 0.07$) but higher than during the non-breeding period (Fig. 3; $t_{23} = 1.773$, $p = 0.09$). Therefore, the males appeared to work hardest during the post-fledging period.

The MDD of the mates in paired surveys tended to be positively correlated during the non-breeding season but not during the post-fledging season (Fig. 4). In 12 paired surveys during the non-breeding season, the proportional time the mates spent vocalising adjacent nights were positively correlated ($r_s = 0.646$, $p = 0.023$) and were equal among the sexes (Wilcoxon's signed rank test, $Z = 0.934$, $p = 0.37$). In 11 paired 3-h surveys during the post-fledging period, the males attended chicks 0.44 ± 0.13 times per hour ($\bar{x} \pm SE$) and females, 0.09 ± 0.05 (Wilcoxon's signed ranks test, $Z = -2.254$, $p = 0.024$). The sample size did not allow any analysis of how feeding rate varied during the post-fledging period, but it appeared that the females primarily provided food to the young during the first month after fledging. In comparison, the males seemed to sustain the feeding intensity and showed extensive movement throughout the post-fledging period.

Home range size

Males and females had equal home range sizes in the non-breeding season (paired t-test: $t_7 = 0.568$, $p = 0.59$). During the post-fledging period, males increased their ranges whereas the females did not (Table 4, Fig. 5). Hence, during the post-fledging period, males had, on average, a 46% larger range than their mates ($t_6 = 2.550$, $p = 0.043$).

Distance to offspring

The females stayed close to their offspring both day and night until 11 d after fledging, whereas the males did not (Fig. 6, Table 5). During the late nesting period, MPOD at night increased with decreasing chick condi-

Table 2. ANCOVA model explaining log[body weight] of tawny owls (first record from 12 males and 21 females) by the effects of log[wing length], body condition (score from 1 to 5) and sex. As shown by the Type-I SS, body condition and sex improves the overall model fit considerably even after the effects of the effect of log[wing length] have been accounted for: ΔR^2 is the additive variation in the dependent variable explained by a factor upon the variation explained by all preceding factors. In contrast, the elimination of the effect of log[wing length] does not significantly deteriorate the fit of the final model. The predicted body mass by the three independent factors is log[body weight, g] = 0.646 + 0.819(log[wing length, mm]) + 0.035(condition score, 1–4) − 0.069(x, x = 1 for males and 0 for females). The function explains 83.5% of the variation in log[body weight]. There were no significant interaction terms (all P-values > 0.6).

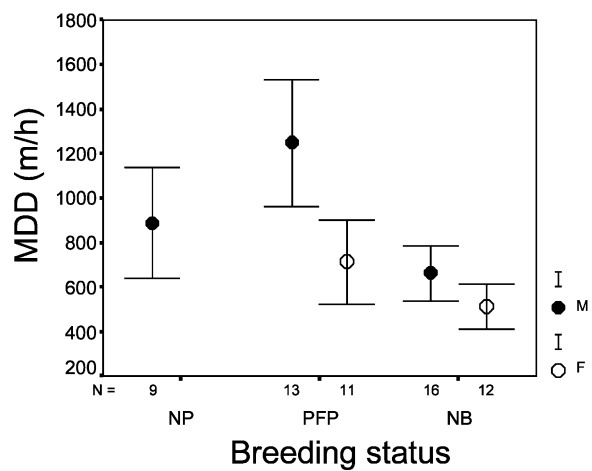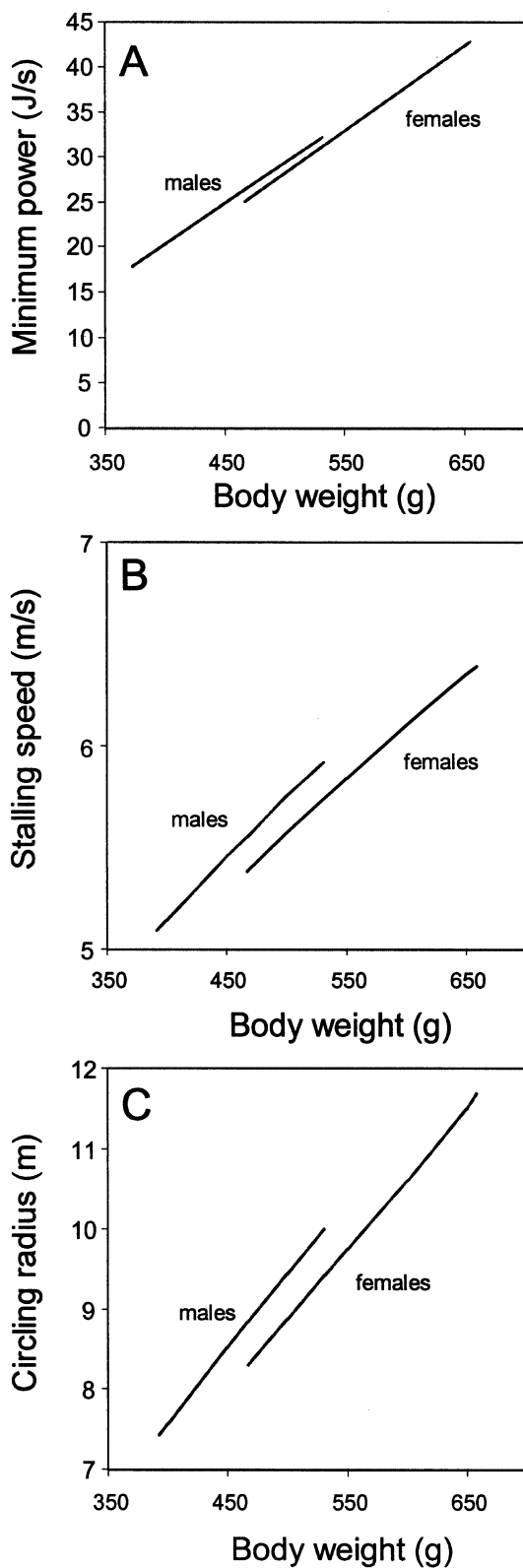|	Type-I sum of squares				Type-III sum of squares		
	df	F	P	ΔR^2	df	F	P
Log[wing length]	1,29	60.372	<0.0001	0.343	1,29	2.914	0.099
Condition score	1,29	50.547	<0.0001	0.287	1,29	26.089	<0.0001
Sex	1,29	36.076	<0.0001	0.205	1,29	36.076	<0.0001

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Fig. 3. Minimum displacement distance (MDD) per time unit of males and females in 3-h surveys during the nesting period (NP), post-fledging period (PFP) and the non-breeding season (NB). The bars indicate 95% confidence intervals of the mean. N indicates the number of surveys. See Table 3 for statistics.

tion in both sexes, but the differences were only significant with respect to females (Fig. 7A). The first 10 d after fledging, MPOD for males showed a significantly negative correlation with chick condition, whereas MPOD for females showed only tendencies (Fig. 7B). When using each telemetry fix as an observation unit during the first 21 d after fledging, the POD in females decreased with decreasing brood age and brood vulnerability and increased with increasing levels of food stress of the brood (Table 6). The females, therefore, appeared to balance their efforts between offspring guarding and foraging. For males, POD also increased with decreasing brood condition, but no response was found with respect to brood age or brood vulnerability (Table 6).

Habitat use and diet composition

Males tended to use denser tree vegetation slightly more than their mates but the difference was far from significant (Fig. 8; compositional analysis: Wilk's $\lambda = 0.68$, $F_{7,2} = 1.66$, $p = 0.26$; paired t-test: $t_8 = 1.61$, $p = 0.15$).

Fig. 2. The flight characteristics of males and females based on mean-values of wingspan and wing area obtained from this study (Table 1) as a function of weight. The lines indicate the observed weight ranges for males (392–531g) and females (467–659g). (A) Minimum power (metabolic) required flying. The functions were virtually identical in the two sexes (difference: 0.2–0.4 J/s), the separation of the lines are somewhat exaggerated in the graph for clarity. (B) Stalling speed, i.e. the speed that keeps an owl gliding for as long as possible. (C) Circling radius, a measure of the ability of a soaring bird to exploit a narrow thermal. Here used as an index of manoeuvrability of a bird not flapping with the wings. The calculations were done by means of the program "Flight.bas", using default values for a non-passerine bird at sea level.
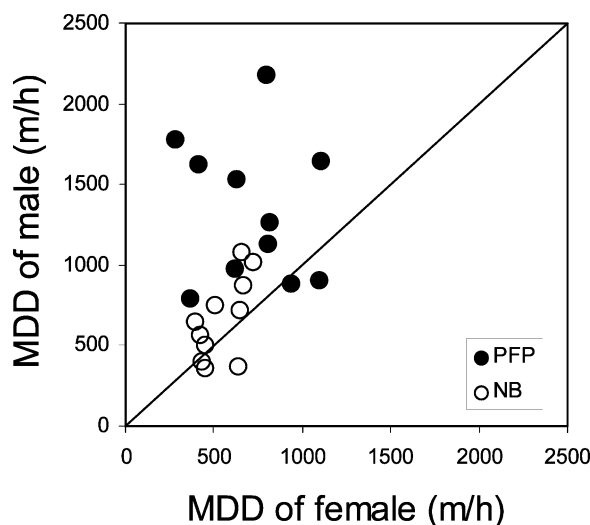
Fig. 4. Minimum displacement distance (MDD) per time unit in paired 3-h surveys of mates on consecutive nights. The MDD of the mates tends to be positively correlated in the non-breeding season (NB: $r_s = 0.573$, $n = 12$, $p = 0.051$) but not during the post-fledging period (PFP: $r_s = -0.118$, $n = 11$, $p = 0.72$). In both periods, males have a higher MDD than females (Wilcoxon's test, NB: $Z = 1.961$, $p = 0.050$; PFP: $Z = 2.667$, $p = 0.008$). If MDD was not influenced by sex, the observations should be equally spaced on each side of the line $y = x$.

Table 3. The effects of sex, breeding status (post-fledging period vs non-breeding period) and pair ID (random factor) on minimum displacement distance (MDD) in 3-h surveys. No other higher order interactions than sex × breeding status were significant. The F-statistics are based on Type-III sum of squares.

		df	F	P
Both sexes	Sex	1,37	20.130	<0.0001
	Breeding status	1,37	22.926	<0.0001
	Sex × Breeding status	1,37	4.687	0.037
	pair ID	9,37	1.087	0.40
Males	Breeding status	1,16	19.080	0.0005
	pair ID	9,16	0.842	0.59
Females	Breeding status	1,12	10.016	0.008
	pair ID	9,12	2.364	0.083

In total, paired diet data from the same period were available from 6 pairs, comprising a total of 380 prey items (Appendix A). Males appeared to eat birds and bats more often than did the females (Fig. 9A, partial sex-by-prey type association from a saturated log-linear model: $\chi_2^2 = 7.952$, $p = 0.019$). However, this impact was minor compared with the differences between pairs (pair-by-prey type association: $\chi_{10}^2 = 76.066$, $p < 0.0001$). Moreover, a significant pair-by-sex-by-prey type interaction ($\chi_{10}^2 = 39.720$, $p = 0.0001$) further indicated that much more of the variation was explained by individual preferences than by a general sex effect. If the individual diet composition by biomass was used as a statistical unit, there was no evidence for sex-

Table 4. The result of repeated measures ANOVAs of the effects of sex and breeding status on 95%-kernel home range size during the post-fledging period and the succeeding post-breeding period until 1 October. The analysis comprising both sexes is based on 6 pairs where both mates were surveyed throughout both periods. The analyses divided by sex (equivalent to paired t-tests) are additionally based on two males and two females with missing or incomplete mate information. The analyses are based on range size measures that were square root-transformed in order to achieve normality and variance heterogeneity. The F-statistics are based on Type-III sum of squares.

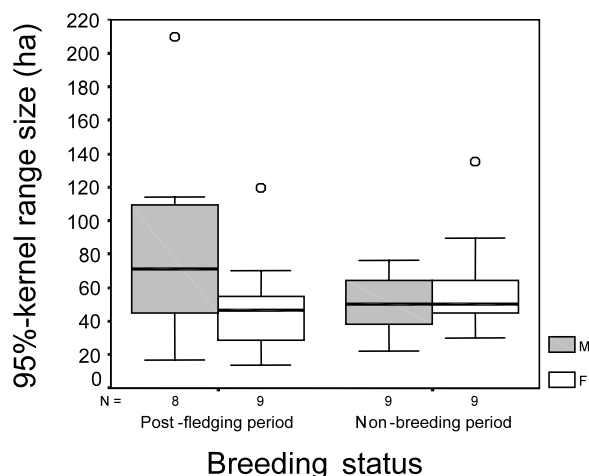|	Variable	df	F	P
Both sexes	Breeding status	1,5	1.789	0.24
	Sex	1,5	4.921	0.077
	Breeding status × Sex	1,5	21.772	0.006
	Pair ID	9,5	13.437	0.005
	Breeding status × Pair ID	9,5	5.853	0.033
Males	Breeding status	1,7	4.754	0.066
Females	Breeding status	1,7	1.497	0.26

Fig. 5. Box plots of 95%-kernel home range size of males and females during the post-fledging period (April–July) and the post-breeding period (from independence of offspring through October). See Table 4 for test statistics.

determined diet segregation (Fig. 9B; compositional analysis: Wilk's $\lambda = 0.80$, $F_{4,2} = 0.50$, $p = 0.64$), nor did the sexes differ in the mean or median weight of the vertebrate prey (Wilcoxon's tests, $Z = 0.135$ $p = 0.89$ and $Z = 1.342$, $p = 0.18$, respectively).

Discussion

Inferences from morphometric measures

The sexual dimorphism was clearly not isometric among different morphological measurements. This indicates the disruptive selection pressures of males and females varied in strength among different morphological traits. Hence, after having corrected for size and

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condition, females were still 16% heavier than males, indicating selection for males being lighter than females or females being heavier than males. Accordingly, the flight calculations showed that males were considerable more energy efficient than the females and apparently more agile fliers as well. To our knowledge, the only other study that has statistically separated the difference between structural size measures and body weight (Marcström and Kenward 1981), also found goshawk (*Accipiter gentilis*) females to be disproportionately heavier than males. Additionally, the food niche segregation hypothesis was supported by the very large dimorphism in the hind claw diameter, as the hind claw is a central part of the killing apparatus (Darwin 1871, Temeles et al. 2000).

Hence, the relative difference in RSD of various morphometric traits gives support for the reproductive role division hypotheses as well as the niche segregation hypotheses.

Observational evidence of reproductive role division

Clear evidence was found for reproductive role partitioning beyond the incubation phase as the sexes differed in all behavioural parameters investigated during the post-fledging period: MDD and chick attention rate, home range size and distance to offspring. All these parameters point towards males playing the dominant role as food providers throughout the breeding season. In addition, it is worth noting that males, in accordance with flight economics, had a higher MDD than females. This is also true during the non-breeding period. Since the sexes did not differ in vocalisation frequency or range size, the observed difference in MDD during the non-breeding season is therefore most likely to be due to lower energetic costs of male flight. The dimorphism in body weight therefore appeared to be large enough to cause a measurable difference in sex-specific foraging behaviour even in the non-breeding season. Even though both sexes had a higher MDD during the post-fledging period as compared to the
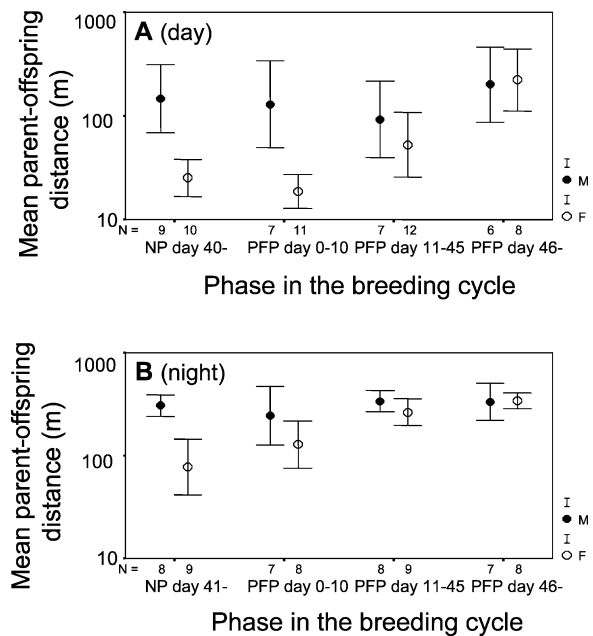

Fig. 6. Mean parent–offspring distance (95% error bars, note the logarithmic scale) at (A) daytime and at (B) night during different phases of the breeding cycle: NP = nesting period (from estimated date of first laid egg) and PFP = post-fledging period (from fledging of the first chick). N is the number of individuals contributing with mean distances to young. For test statistics, see Table 5.

non-breeding season, this increase was disproportionately higher in males, indicating a disproportionately high foraging effort by males during the post-fledging season. Since males also attended fledged chicks more often than females and increased their foraging range during the post-fledging period, it should be safe to conclude that the male played a more important role in raising the brood even after the female's incubation duties were completed. The females, in contrast, stayed much closer to the brood when the chicks were young, clearly guarding the brood, harassing potential predators (foxes, humans) that approached the young during that period (see also Wallin 1987). The first few weeks after fledging the young frequently appear on or near

Table 5. Repeated measures ANOVA of the effects of the four breeding phases (within-subject comparison) and sex (between-subject comparison) on mean parent–offspring-distance (MPOD, log-transformed data). The breeding phases are defined as in Fig. 6. The F-statistics are based on Type-III sum of squares. As no variation in MPOD existed among the pairs (both P-values > 0.4) in the few pair-observations, this variable was skipped from both models in order to increase the number of degrees of freedom.

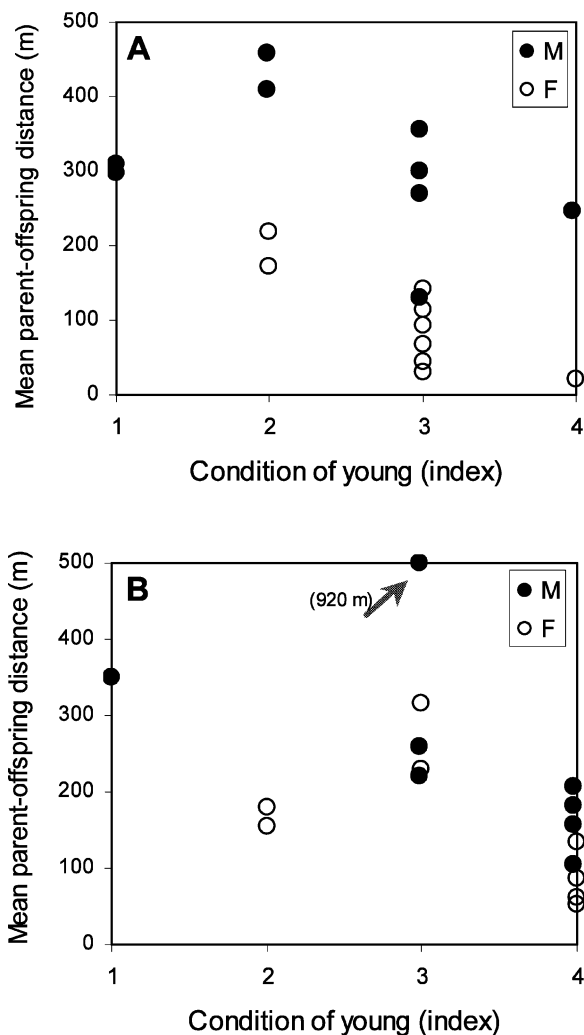|		Day (9 males, 7 females)			Night (4 males, 5 females)		
		df	F	P	df	F	P
Both sexes	Breeding phase	3,42	7.975	0.0003	3,21	12.999	0.0001
	Breeding phase × Sex	3,42	5.708	0.002	3,21	6.022	0.004
	Sex	1,14	3.751	0.07	1,7	4.141	0.08
Males	Breeding phase	3,24	0.924	0.44	3,9	1.728	0.23
Females	Breeding phase	3,18	11.490	0.0002	3,12	16.479	0.0001

Fig. 7. Mean parent–offspring distance at night plotted against the level of food stress in the brood (1: chicks starved to death – 4: all chicks well nourished. As the lowest scores are only represented in males, score 1 and 2 receive the same rank in the correlation analyses) during (A) the late nesting period (later than 40 days after incubation start; males: $r_s = -0.648$, $n = 9$, $p < 0.10$; females: $r_s = -0.837$, $n = 9$, $p < 0.01$) and (B) day 0–10 after fledging (males: $r_s = -0.861$, $n = 8$, $p < 0.05$; females: $r_s = -0.720$, $n = 8$, $p < 0.10$). The arrow in (B) indicates an extreme value.

the ground. Since 20–25% of the chicks fall prey to predators during this period (Petty and Thirgood 1989, Coles and Petty 1997, Overskaug et al. 1999, Sunde 2001), brood guarding may be an adaptive behaviour during the first critical weeks of the post-fledging period. The negative correlation between MPOD at night and nestling condition indicates that the females balanced their effort between foraging and offspring guarding. Further evidence of this suggestion was found in the analysis based on individual spot observations, showing that the POD of females the first three weeks after fledging decreased with vulnerability and

increased with food stress in the brood. Therefore intensified guarding of fledglings vulnerable to predation probably explains the apparent lack of correlation between MPOD and brood condition in females. Since males with hungry chicks also foraged farther away from the offspring, they also might adjust their foraging efforts to the energetic need of their brood but in contrast to females, their MPOD did not correlate with the vulnerability of the brood. However, variation in MPOD is more difficult to evaluate in males than in females because they foraged farther away from the brood and therefore were more likely to be constrained by territory borders, as indicated by the significant difference in POD among males but not among females. Accordingly, variation in MPOD in males could therefore also just reflect differences in territory size and habitat quality.

No observational evidence of resource partitioning

In spite of the observed dimorphism in the hind claw diameter, no consistent diet difference between the sexes was found, either in mean or median prey mass or in overall diet composition. This result is in line with an investigation of the stomach content of Norwegian tawny owls (Overskaug et al. 1995) that found a tendency towards males taking marginally larger prey items than females. Our investigation also shows that diet analyses using prey items as statistical units can be severely biased by individual preferences and should therefore be based on the individual predator or pair as the observational unit (see also Korpimäki et al. 1994). It should be also be noted that our diet data primarily originates from the non-breeding season, and the possibility may exist that females would specialise in large prey items only during the breeding season (van Veen and Kirk 2000).

Since the sexes had a similar habitat usage with respect to canopy closure, no evidence was found for dimorphism in morphological characters to correlate with differential resource exploitation. As no cases of intra-pair aggressions were recorded during the radio tracking, it is also highly unlikely that the female should displace the male from certain habitat types. In conclusion, no support for the resource-partitioning hypothesis was found in the tawny owl.

Possible selective mechanisms for reproductive role division in the tawny owl

We found evidence for a high degree of labour division in the breeding effort after the incubation state, with the male playing the role as main food provider and the female as main brood guard, whereas no sign of resource partitioning of the pairs was found. Hence, the

Table 6. ANCOVA-models of the influence of brood age (in days after fledging), roosting height (m) of the lowest sitting chick in the brood and of brood condition on parent–offspring distance (POD, log transformed distance in meters) at night during the first 3 weeks after fledging. Brood condition is scored on an index from 1 (occurrence of starvation mortality) to 4 (all chicks well fed). In model I, a possible inter-pair difference is tested by using the pair ID as a random factor. In model II, the effect of pair ID is replaced by the effect of brood condition (confounding with pair ID). The significance of model II for males is dubious due to a significant inter-pair difference. The F-statistics are based on Type-III sum of squares. B gives the parameter values for the predicted relations. No higher order interactions were significant (all P-values > 0.15).

		Males				Females			
		df	F	P	B	df	F	P	B
Model I	Days since fledging	1,55	0.168	0.68	0.0035	1,40	7.204	0.011	0.0281
	Altitude of chicks	1,55	2.656	0.11	0.117	1,40	9.851	0.003	0.0325
	Pair ID	9,55	2.397	0.023	0–0.784	10,40	1.439	0.20	−0.423–0.422
	Constant				1.792				1.472
Model II	Days since fledging	1,63	1.920	(0.17)	0.0196	1,49	7.645	0.008	0.0268
	Altitude of chicks	1,63	0.164	(0.69)	0.0025	1,49	11.165	0.002	0.0275
	Condition of young	1,63	3.961	(0.051)	−0.162	1,49	5.499	0.023	0.205
	Constant				2.595				1.961

reasons for RSD in the tawny owl should be found in the reproductive role division of the sexes. The question is then whether RSD is maintained by natural selection, by keeping males smaller and lighter than optimal for their survival chances during the non-breeding period, females larger and heavier or both.

As males expressed significant responses in all measured parameters related to foraging effort, it is probable that males are selected to be light and efficient foragers during the breeding season. The finding that the MDD of males appeared to be higher during the post-fledging period than during the nesting period further indicates that the energy investment in the foraging effort by the male was no lower during the late half of the breeding season than in the early half when
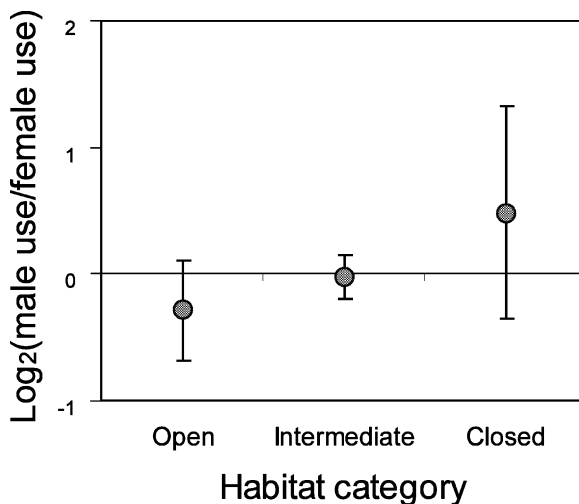

Fig. 8. Relative sex difference in habitat use of 9 tawny owl pairs, measured as the log-odds (means and 95% error bars) of the proportional use of the three vegetation density categories. A mean $\log_2$-odds value of 0 indicates no overall sex difference, a value of 1, that the category is used twice as much by males than by females; a value of 2, a four-fold preference etc.

the female was confined to the nest. As an alternative to selection for small/light male size, increased starvation resistance of incubating females through large body size has been suggested as a selective mechanism for large female body size (Lundberg 1986). Starvation endurance is a crucial parameter for incubation success in the tawny owl (Hirons 1985a), but since the females begin incubating on lower fat reserves in poor years than in good years (Hirons et al. 1984, Hirons 1985a), their fat storing capacity is apparently not limited by their body size in those years when starvation buffers are most important for successful incubation. Neither have consistent correlations between reproductive success and female body size been found in Tengmalm's owls (Hakkarainen and Korpimäki 1991, 1993) or kestrels (Massemin et al. 2000).

Even though it is likely that large body size is advantageous for successful brood defence, the defence level of tawny owl females has been found not to correlate with absolute size (Wallin 1987). Rather, as the mate with the poorest foraging potential, the female is predetermined to take the job of guarding the young. The possibility exist, though, that the more robust hind claws of females is an adaptation to defence behaviour against mammalian and avian predators that are far beyond normal prey size.

Conclusion

Due to the lack of ecological segregation between the sexes, we conclude that inter-specific food competition is unlikely to be a selective factor contributing to RSD in the tawny owl. Owing to males being smaller and also proportionally lighter than females and supported by the observational data on differential breeding effort, we find it most likely that the RSD in tawny owls is maintained by selection for reproductive role division. As the tawny owl is an extreme example of a
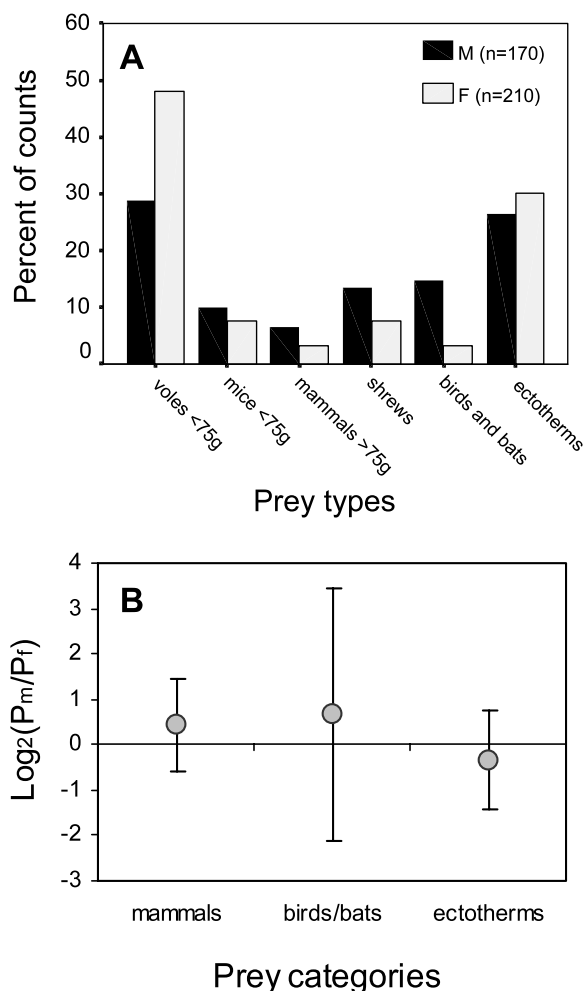
Fig. 9. Diet composition of 6 tawny owl pairs shown as (A) the total percentage distribution of prey types of males and females (n = number of prey items, see Appendix A) and as (B) the relative differences in diet composition weighted by biomass measured as log-odds (means and 95% error bars). A mean log-odds value of 0 indicates no overall sex difference, a value of 1 that the category is used twice as much by males than by females; a value of 2, a four-fold preference etc. P_m = proportion of the male's diet made up of a given prey category, P_f = proportion of the female's diet made up of a given prey category.

species where a breeding pair's foraging range is confined by territoriality, our study provides further evidence for selection for differential breeding effort, probably on males being lighter and energetically efficient foragers, is the general evolutionary force behind RSD in raptorial birds, even when the potential benefits of food niche segregation should be obviously advantageous.

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Appendix. Sex-specific diet composition estimated from pellets collected at the same time for mates, given as frequency of prey items (*n*) and estimated percentage of the total biomass for each mate (%mass). Data on biomass are based on information from our own data on body masses of small mammals trapped in the area and from handbook data (Niethammer and Krapp 1978–1990). Samples partially collected throughout the post-fledging period are indicated with (*).

Pair ID	sex	Period	Voles <75g		Mice <75g		Mammals >75g		Shrews		Birds/bats		Amphibians/ invertebr.		Total	Vertebrate prey weight (g)	
			n	%mass	*n*	%mass	*n*	%mass	*n*	%mass	*n*	%mass	*n*	%mass	*n*	mean	median
1*	M	May–July	0	0	0	0	5	52	14	5	9	35	18	8	46	35	6
	F	2000	2	19	0	0	1	59	2	2	1	14	3	6	9	28	5
2	M	June–July	4	15	4	20	1	25	0	0	4	23	6	17	19	33	24
	F	1999	29	54	1	2	3	36	1	1	0	0	4	7	38	33	24
3	M	June–Aug	6	26	0	0	1	33	4	5	7	23	15	12	33	17	15
	F	2000	4	32	0	0	0	0	4	10	0	0	27	58	35	9	5
4	M	Sept–Nov	12	42	6	28	1	24	1	1	0	0	4	5	24	26	24
	F	1999	16	33	10	28	2	28	1	0	2	7	9	4	40	28	24
5	M	April–June	15	85	2	15	0	0	0	0	0	0	0	0	17	23	24
	F	2000	49	74	5	10	1	10	7	3	1	1	17	3	80	22	24
6*	M	May–Aug	12	30	4	11	3	49	4	3	5	7	2	1	30	32	24
	F	2000	1	10	0	0	0	0	1	3	3	87	3	0	8	47	24