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Abstract Reversed sexual dimorphism (RSD), which occurs when the female of a species is larger than the male, is the rule for most birds of prey but the exception among other bird and mammal species. The selective pressures that favour RSD are an intriguing issue in animal ecology. Despite the large number of hypotheses proposed to explain the evolution of RSD, there is still no consensus about the mechanisms involved and whether they act on one or both sexes, mainly because few intrapopulation studies have been undertaken and few raptor species have been investigated. Using the strongly size-dimorphic northern goshawk (*Accipiter gentilis* L.) as a model, we studied a population with one of the highest densities of breeding pairs reported in the literature in order to understand selective pressures that may favour RSD. We evaluated life-history processes, including recruitment of adult breeders and reproductive success, and we explored the mechanisms thought to act on each sex, including hunting efficiency, diet, body condition and mate choice. We found that smaller males produced more fledglings than larger ones, but there was no relationship between size and reproductive success for females. The mean body size of female breeders was larger than that of female fledglings, but male fledglings and breeders did not differ in size. Male body size was related to the type but not to the amount of prey captured during the nestling stage. We conclude that RSD may be favoured in this goshawk population because small males tend to enjoy higher reproductive success and large females greater recruitment. Our results do not support the hypothesis that evolutionary reduction in male size is driven by hunting efficiency, at least during the nestling stage, or the hypothesis that it is driven by greater recruitment. Our findings also suggest that increase in female size is driven by recruitment, rather than by reproductive success as previously postulated.

Keywords (separated by '-') *Accipiter gentilis* - Bird of prey - Body size - Evolution - Raptor

Footnote Information Communicated by Markku Orell.
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Electronic supplementary
material

Below is the link to the electronic supplementary material.

MOESM1: Supplementary material 1 (PDF 107 kb).

2 **Higher reproductive success of small males and greater**
3 **recruitment of large females may explain strong reversed sexual**
4 **dimorphism (RSD) in the northern goshawk**

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6 S. Martínez-Hestekamp · J. M. Fernández-Pereira

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Introduction

Reversed sexual dimorphism (RSD), in which the females
of a species are larger than the males, arose from differ-
ences in male and female evolutionary processes (Reynolds
1972; Andersson and Norberg 1981; Kenward 2006). RSD
may arise because of an evolutionary increase in female
size, a reduction in male size or a divergence in size of the
two sexes (Ydenberg and Forbes 1991), but this question
is still unsolved. While the persistence of RSD in raptors
must be the result of processes that confer adaptive advan-
tages that enhance reproductive success and/or recruitment,
we do not know yet which of these processes affect each
sex. The mechanisms behind such processes that under-
lie the evolution of RSD have been the subject of much
theorising, leading to numerous hypotheses over the last
50 years but no consensus. Although many of the suggested

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61 hypotheses explain potential advantages of RSD, most fail
62 to explain why the dimorphism occurred in reverse form
63 (larger females) rather than the conventional form (larger
64 males) (Kenward 2006).

65 Hypotheses to explain the origin and maintenance of
66 RSD can be arranged into two categories depending on the
67 major process they involve: reproductive success hypoth-
68 eses and recruitment hypotheses. Among the reproductive
69 success hypotheses, one of the most accepted ideas states
70 that the raptorial lifestyle may be crucial for explaining
71 the origin of RSD (Walter 1979). Many raptors hunt and
72 capture prey in a violent and strenuous way that may be
73 harmful to eggs during egg formation. This may have led
74 to a sex role differentiation in which the female must avoid
75 hunting at least until egg laying, while the male must hunt
76 and provide food for his mate. In this scenario, any mor-
77 phological change that enhances the efficiency with which
78 either sex performs its roles should improve reproductive
79 success (Storer 1966). The nimble male hypothesis pre-
80 dictes that small males have greater aerial agility and hence
81 greater hunting ability than large ones, allowing small
82 males to more effectively capture small prey, which are
83 usually more abundant (Storer 1966; Newton 1979). Addi-
84 tionally, we think that the greater aerial agility of small
85 males may make them more efficient hunters in structur-
86 ally complex environments such as forests. The result-
87 ing greater reproductive success of smaller males should
88 lead to a progressive reduction in male size (Storer 1966;
89 Reynolds 1972; Ydenberg and Forbes 1991). On the other
90 hand, the big mother hypothesis predicts that large females
91 can store more energy for egg production, allowing them
92 to produce more eggs that also have larger reserves, and
93 that large females can more effectively incubate the eggs
94 in their nests, leading them to enjoy greater reproductive
95 success. This should lead to an increase in female size
96 (Selander 1966; Reynolds 1972; Kenward 2006). Thus, the
97 nimble male and big mother hypotheses may hold the key
98 to explaining the origins of RSD among raptors because
A Q 2 they specifically predict the reversed dimorphism (see Mas-
100 semin et al. 2000; Krüger 2005 for a review of hypotheses
101 on RSD).

102 As most raptor species are territorial (Newton 1979),
103 breeder recruitment may be limited by survival and/or ter-
104 ritory acquisition. Among the recruitment hypotheses, the
105 male competition for territory and male competition for
106 mate hypotheses postulate that the smaller the male, the
107 greater his aerial agility to compete more effectively with
108 other males for access to a nesting territory and a mate
109 through acrobatic aerial displays (Widén 1984; Figuerola
110 1999). On the other hand, the female competition for ter-
111 ritory and female competition for mate hypotheses pos-
112 tulate that the larger the female, the greater her effective-
113 ness at competing with other females for good mates and

the nesting territories they own (Olsen and Olsen 1987;
McDonald et al. 2005).

It is difficult to test most of these hypothetical mecha-
nisms rigourously in the field (Andersson and Norberg
1981; Krüger 2005), so there is a lack of intrapopulation
studies, and few raptor species have been studied in depth
(Newton 1989; Hakkarainen and Korpimäki 1991; Mas-
semin et al. 2000; McDonald et al. 2005; Sergio et al. 2007,
among others). As a result, whether the aforementioned
hypotheses can explain the origin and maintenance of RSD
in raptors remains uncertain. In this way, complementing
classical species comparison studies with intrapopulation
studies may prove an effective way to illuminate the pro-
cesses that drive RSD (Tornberg et al. 1999).

The northern goshawk (*Accipiter gentilis* L., hereafter
“goshawk”) is a long-living, medium-sized, forest-dwell-
ing raptor that shows strong territorial behaviour and high
mate and territory fidelity (Squires and Reynolds 1997;
Kenward 2006). It is distributed extensively throughout
the Holarctic region, where it preys upon a wide variety of
small- and medium-sized birds and mammals (Cramp and
Simmons 1980; Squires and Reynolds 1997; Rebollo et al.
2010, 2011; Krüger et al. 2012). Goshawks exhibit a sig-
nificant RSD, with females exceeding males by 12.5 % in
wing length and 61 % in mass (Kenward 2006). In addi-
tion, mean body size in goshawk populations can change
surprisingly quickly (Yom-Tov and Yom-Tov 2006). In
fact, Tornberg et al. (1999) suggested that a dietary shift
increased goshawk RSD in northern Finland in only three
decades. These last two characteristics make the goshawk
a powerful model for understanding the evolution of RSD
(Reynolds 1972).

In the present work, we studied a dense goshawk popu-
lation in the NW Iberian Peninsula. Two of our aims were
to assess whether one or both sexes are affected by the
processes that may favour RSD, and whether body size
influences reproductive success. We hypothesised that
the mechanisms behind the nimble male and big mother
hypotheses continue to act on this population (Table 1).
Our third aim was to assess whether body size influences
breeder recruitment. We hypothesised that the mechanisms
behind the competition for mate hypotheses continue to act
on this goshawk population (Table 1).

Materials and methods

Study area and species

The study was carried out for four years (2008–2011) in
the Morrazo Peninsula and inland adjacent area (~400 km²)
in NW Spain (latitude 42°20'N, longitude 8°47'W). It is
an area of rough topography at a mean altitude of 213 m,



Table 1 Study hypotheses and the variables used to test them

Hypothesis	Explanatory variable	N	Response variable	N
Reproductive success hypotheses				
Nimble male hypothesis				
(1) Small males have greater reproductive success (more fledglings)	Male body size (PC1)	33	Fledgling number/nest	33
(2) Small males have better body condition	Male body size (PC1)	19	Male weight/male tarsus length	19
(3) Small males capture more prey	Male body size (PC1)	29	Number of prey carried to the nest/day	29
(4) Small males capture smaller prey	Male body size (PC1)	29	Mean prey size	29
(5) Small males capture more forest prey	Male body size (PC1)	29	% forest prey	29
(6) Small males capture less non-forest prey	Male body size (PC1)	29	% non-forest prey	29
Big mother hypothesis				
(7) Large females have greater reproductive success (more fledglings)	Female body size (PC1)	41	Fledgling number/nest	41
(8) Large females have better body condition	Female body size (PC1)	27	Female weight/female tarsus length	27
Recruitment hypothesis				
(9) Small males have greater recruitment	Male fledgling tarsus length ^a	19	Male breeding tarsus length ^a	21
(10) Large females have greater recruitment	Female fledgling tarsus length ^a	20	Female breeding tarsus length ^a	19
Competition for mate hypothesis				
(11) Small males and large females tend to mate	Male body size (PC1)	12	Female body size (PC1)	12
(12) Couples formed by small males and large females have greater reproductive success (more fledglings)	Intra-pair dimorphism index	17	Fledgling number/nest	17

Hypotheses 2–6 and 8 were assessed during the nestling phase

N number of samples

^a In hypotheses 9 and 10, the two specified variables are compared, i.e. there is neither an explanatory nor a response variable

163 with altitude ranging between 0 and 646 m. The climate is
 164 oceanic-humid with a tendency for summer droughts. Aver-
 165 age annual precipitation is 1,586 mm and average annual
 166 temperature is 14.4 °C (Carballeira et al. 1983). Winter is
 167 mild: it does not snow and temperatures rarely fall below
 168 0 °C. Approximately 49 % of the study area is open, mostly
 169 cultivated land and meadows, while the remainder (51 %) is
 170 covered by eucalyptus plantations (*Eucalyptus globulus*
 171 Labill.) often mixed with oak (*Quercus robur* L.) and pine
 172 (mainly *Pinus pinaster* Ait.).

173 The goshawk breeding population in the study area shows
 174 one of the highest densities reported in the literature (annual
 175 average of 10.0 egg-laying pairs/100 km²) and a mean pro-
 176 ductivity of 2.3 fledged young/laying pair. The goshawk diet
 177 consists of species living in forest (hereafter forest prey),
 178 open-land (non-forest prey) and mixed habitats (other prey).
 179 Forest prey (39 % overall) comprise Eurasian jay (*Garrulus*
 180 *glandarius* L., 16.8 %), green woodpecker (*Picus viridis* L.,
 181 10.4 %), Eurasian red squirrel (*Sciurus vulgaris* L., 8.5 %),
 182 and great spotted woodpecker (*Dendrocopos major* L.,
 183 3.7 %); non-forest prey (35 % overall) include feral pigeon
 184 (*Columba livia f. domestica* Gmelin, 17.1 %), Eurasian col-
 185 lared dove (*Streptopelia decaocto* Frivaldszky, 10.8 %) and
 186 the common magpie (*Pica pica* L., 7.2 %); and other prey
 187 comprise 27 species (26 % overall) (unpublished data). This
 188 last group was not considered in our study because it is not
 189 directly relevant to testing the effects of hunting habitat on
 190 RSD (Table 1; hypotheses 5 and 6).

191 Field procedures and measurements

192 In each year of the study period, the study area was inten-
 193 sively searched to locate all existing goshawk nests. A total
 194 of 41 active goshawk territories were found. We climbed
 195 up to the nests when nestlings were older than 20 days
 196 (24.6 ± 4.19 days, mean \pm SD), when they can completely
 197 self-thermoregulate and feed themselves (Kenward 2006;
 198 Byholm et al. 2011). A total of 210 nestlings were meas-
 199 ured and tarsus-ringed with field-readable coloured alu-
 200 minium rings with a two-character alphanumeric code. A
 201 digital photo camera (Moultrie I40 digital game camera)
 202 was installed in every nest in order to monitor the frequen-
 203 cies and types of prey supplied to the nests. These cameras
 204 were equipped with a passive infrared sensor that trig-
 205 gered image capture whenever motion was detected, with
 206 a minimum delay of 1 min between images. The average
 207 operating time of the cameras was 44.8 days per year, and
 208 each took a mean of 6,143 pictures per nest and year. In
 209 addition, during the breeding season, we placed cameras
 210 on the ground near each nest and baited them with a caged
 211 chicken to identify breeding adults. The cage was anchored
 212 to the ground and the chicken was adequately protected
 213 from predators and provided with water and food.

214 To capture the breeders of every territory, we used Dho-
 215 gaza nets and a radio-controlled, stuffed, two-movement
 216 Eurasian eagle-owl (*Bubo bubo* L.) as a decoy bird. We
 217 also used owl and goshawk playback calls to attract the
 218 goshawks when they were not near the nests. Trapping was
 219 only attempted in favourable weather conditions and when
 220 nestlings were 3–5 weeks old (Zuberogoitia et al. 2008).
 221 We trapped 39 different breeding individuals (19 males and
 222 20 females). Trapped goshawks were measured, weighed
 223 and ringed with field-readable rings. We identified ringed
 224 breeders in subsequent years either by recapturing those
 225 (11 identifications) or using data from the cameras placed
 226 in the nests or on the ground (40 identifications). In the
 227 end, 90 identifications were made throughout the four years
 228 of the study through captures, recaptures and photographic
 229 identification. When a goshawk was identified in photo-
 230 graphs but not captured in a given year, we used its most
 231 recently recorded morphological measurements in the data
 232 analysis. However, we did not use previously recorded
 233 weight, as this can vary significantly from year to year.

234 We used the number of nestlings at the time of ringing as
 235 a variable to represent reproductive success. Brood size at
 236 this time describes the number of fledged young fairly well
 237 since most nestling mortality occurs soon after hatching
 238 (Kostrzewa and Kostrzewa 1990; Mañosa 1991; Byholm
 239 2005). We measured tarsus width at the narrowest point
 240 of the tarsus in order to sex nestlings and breeders (males
 241 <6.5 mm, females >6.5 mm; Kenward 2006). Length of the
 242 seventh primary feather was measured to estimate nestling
 243 age (Mañosa 1994). Tarsus length, defined as the length of
 244 the metatarsal bone from the toe joint to the notch of the
 245 tarsus–tibia joint, was measured in nestlings older than
 246 28–29 days (hereafter “fledglings”). Tarsus length was the
 247 only morphological measurement that had stabilised for
 248 both males and females by this age, as previously shown
 249 by Mañosa (1991) (see also Fig. S1 of the Electronic sup-
 250 plementary material, ESM). Thus, in the statistical analyses
 251 we used only one measurement (tarsus length) as a surro-
 252 gate of fledgling body size. Also, among the total of 210
 253 ringed nestlings, we used data from only 31 nestlings (14
 254 male and 17 female) that were old enough to have full-
 255 grown metatarsi at the time of ringing.

256 We defined adult body size separately for males and
 257 females as the first axis of a principal component analy-
 258 sis (PC1, hereafter “body size”) involving the following
 259 variables: wingspan, defined as the distance between the
 260 wing tips after the bird was laid on its back and the wings
 261 extended to form a straight line; head-to-bill length, meas-
 262 ured from the base of the skull to the tip of the bill; and
 263 tarsus length (McDonald et al. 2005; Sergio et al. 2007).
 264 PC1 explained 63 % of the size variation in males and
 265 46 % of that in females, and had high positive loadings for
 266 wingspan (males, $r = 0.77$; females, $r = 0.48$), head-to-bill

length (0.83, 0.72) and tarsus length (0.78, 0.79). We scaled adult mass to body size (mass divided by tarsus length) to generate a body condition index (Bortolotti and Iko 1992). We were unable to use mass residuals or other more accurate body condition indices because we found no relationship between mass and body size in our data.

We estimated the intra-pair degree of dimorphism separately for each of the three dimensions of wingspan, head-to-bill length and tarsus length using the following formula (Storer 1966): $100 \times (\text{female dimension} - \text{male dimension}) / (0.5 \times (\text{female dimension} + \text{male dimension}))$.

The mean value across all three estimates was used as an index of intrapair size dimorphism (hereafter “intrapair dimorphism index”).

The cameras placed in the nests provided data on the following variables: mean number of prey supplied to the nest per day, mean mass of prey, % forest prey, and % non-forest prey. In many cases, we were able to assess the age of prey (nestling, fledgling, adult) with the help of the nest cameras and prey remains collected.

Statistical analyses

We used generalised linear mixed models (GLMMs) to analyse the relationships of body size and intrapair dimorphism index to a set of dependent variables (hypotheses 1–8 and 11–12, Table 1). We used GLMMs with a Gaussian distribution when normality and homogeneity of residual variances of dependent variables were obtained (hypotheses 2–6, 8 and 11). We used GLMMs with a Poisson distribution when the dependent variable corresponded to the number of fledged young (hypotheses 1, 7 and 12). Male and female body size and intrapair dimorphism index were fixed factors in GLMMs testing the different hypotheses. Year, nesting territory and individual identity were included as random factors in GLMMs in order to manage the non-independent nature of the data.

We generated 95 % confidence intervals (CIs) for the standardised coefficients of each model using a bootstrap procedure. We extracted 1,000 bootstrap samples by resampling with replacement pairs of body size or intrapair dimorphism index and dependent variable values from the original dataset. Each bootstrap sample contained the same number of cells as the source data, and GLMM standardised coefficients were recalculated for each sample. With this procedure, we generated 1,000 ranked values per scalar metric, of which the values at the 25th and 976th positions corresponded to the lower and upper limits of the 95 % CI for that metric. When the 95 % CI of a predictor’s coefficient does not include zero, a significant association of that predictor with the response variable is indicated, supporting the hypothesis linked to the predictor. We applied this procedure rather than the significance level usually utilised

in classical parametric statistics because, for relatively small samples such as the 20–40 observations in our study, it reduces the probability of accepting the null hypothesis when in fact the alternative hypothesis is true (type II error).

A two-tailed Student’s *t* test was used to test for significant differences in body size between fledglings and breeding adults. Males and females were evaluated separately (hypotheses 9 and 10). Bootstrapping and GLMM building were carried out using the R package “lme4” (Bates et al. 2011).

Results

Reproductive success hypothesis

Smaller breeding males had higher reproductive success (fledgling production) and better body condition than larger males (Figs. 1, 2a, b; Table 2). However, smaller males did not provide their offspring with more prey than larger ones did, at least during the second half of the nestling phase when we assessed the frequency of prey deliveries. During this period, smaller and larger males supplied prey of similar mean sizes. Taking into account the three categories of prey (forest, non-forest and other preys), smaller males captured a similar proportion of forest prey to that caught by larger males (Eurasian jay, green and great spotted woodpeckers, Eurasian red squirrel) but significantly less non-forest prey (feral pigeon, Eurasian collared dove, common magpie, Fig. 2c). Breeding female size was related to neither fledgling production nor female body condition (Fig. 1).

Recruitment hypothesis

Mean body size in the subpopulation of fledgling females was smaller than that in the subpopulation of breeding females that owned a territory and produced at least one fledgling (Table 3). In contrast, mean body size was similar for fledgling males and breeding males. In addition, the coefficient of variation (CV) of body size was 22 % greater in the subpopulation of breeding males (3.23 %) than in the subpopulation of breeding females (2.64 %), suggesting that breeding females may have been selected based on size during recruitment. Among breeding pairs that raised at least one fledgling, the size of the female was unrelated to the size of the male, and the intrapair dimorphism index was not related to fledgling production (Fig. 1).

Discussion

To our knowledge, the present research is the first providing evidence that selective pressures, acting differently

362 on both sexes, may be favouring RSD in the goshawk, a
 363 strongly size-dimorphic raptor. Our data over the 4-year
 364 study period show that smaller males had higher reproduc-
 365 tive success than larger males and that male recruitment
 366 was not influenced by body size, while the opposite was
 367 true for females: larger individuals were recruited more
 368 often as breeders than smaller ones (Tables 2, 3). Together,
 369 these processes could increase the proportions of small
 370 males and large females in the goshawk population, so
 371 these processes could favour RSD.

372 Reproductive advantages for small males

373 Smaller breeding males produced more fledglings and had
 374 better body condition than larger ones. This is one of the
 375 few studies showing that small body size enhances the
 376 reproductive success of the male in a raptor species (see
 377 also Hakkarainen and Korpimäki 1991; Massemin et al.
 378 2000; Sergio et al. 2007). However, our findings, at least
 379 during the nestling phase, are not in agreement with the
 380 nimble male hypothesis, which argues that smaller males
 381 hunt better due to their greater aerial agility (Storer 1966;
 382 Ydenberg and Forbes 1991; Hakkarainen et al. 1996). As
 383 in most raptor species, male goshawks provide most of the
 384 food during the breeding season, at least from the egg-lay-
 385 ing period until the mid-nestling period (Newton 1979). As
 386 a result, differences in male hunting efficiency should be
 387 translated directly into differences in reproductive success.
 388 Smaller and more agile males should be more efficient at
 389 capturing smaller prey, which are usually more abundant
 390 (Storer 1966). However, contrary to our expectations,
 391 smaller and larger males delivered to nestlings at least
 392 20 days old similar numbers of prey of similar mean sizes
 393 that contained similar proportions of forest prey. Neverthe-
 394 less, we detected differences in prey composition, which
 395 related to male size. Smaller males captured less non-for-
 396 est prey than did larger males (feral pigeon, collared dove
 397 and magpie). This suggests that hunting this type of prey
 398 is more effective when the male is large and therefore has
 399 greater flight power (Alerstam et al. 2007). Indeed, open-
 400 land prey, mainly feral pigeons and doves, are relatively
 401 large with strong flight power (Johnston and Janiga 1995).

402 Based on our result that smaller males produce more
 403 fledglings, and based on male-size-related differences in
 404 hunting skills, we suggest that at a reproductive stage pre-
 405 ceding the one that we studied, smaller males could cap-
 406 ture more prey than larger ones. As a result, smaller males
 407 would show better body condition and greater reproductive
 408 success, as we found. Indeed, smaller male goshawks may
 409 have lower total energy requirements than larger males, so
 410 small males can dedicate a greater proportion of captured
 411 food to their offspring and mate (Reynolds 1972), and
 412 thereby maintain a better body condition. We hypothesise

413 that the critical stage during which small males capture
 414 more prey than large ones may extend from the courtship
 415 to the pre-laying period, when the male must feed its mate,
 416 as pointed out by Newton and Marquiss (1984) for the
 417 highly dimorphic Eurasian sparrowhawk (*Accipiter nisus*
 418 L.). Those authors found that prey populations are at their
 419 minimal annual density during this period and that male-
 420 size-related differences in hunting efficiency become more
 421 pronounced. Later, when fledglings and juveniles of most
 422 prey species are available, hunting becomes easier and
 423 male-size-related differences in hunting efficiency become
 424 less apparent (Quinn and Cresswell 2004). Our diet data
 425 support these findings, showing numerous nestlings and
 426 fledglings of forest prey (65.7 %) but few nestlings and
 427 fledglings of non-forest prey (31.4 %). The high vulnerabil-
 428 ity of nestlings and fledglings, irrespective of raptor size,
 429 may explain why we found male-size-related differences in
 430 non-forest prey captured, but not in forest prey captured.

431 The results of this study do not show that body size
 432 influences male goshawk recruitment, i.e. the overall pro-
 433 cess of survival and acquisition of nesting territory. This
 434 may be because male body size does not affect the individ-
 435 ual processes of survival or territory acquisition, or it may
 436 be because body size affects survival and territory acquisi-
 437 tion in opposite, potentially self-cancelling, ways. Indeed,
 438 Ydenberg and Forbes (1991) suggested that survival selec-
 439 tion in raptors may be counterbalanced by reproductive
 440 selection.

441 Recruitment advantages for large females

442 The big mother hypothesis (Selander 1966; Reynolds
 443 1972; Kenward 2006) was not supported by our results,
 444 as also found in other studies (Mueller and Meyer 1985;
 445 Hakkarainen and Korpimäki 1991; Massemin et al. 2000),
 446 likely reflecting a higher metabolic expenditure for larger
 447 females than for smaller ones (Schoener 1968). Our results
 448 suggest that recruitment may favour larger females. In
 449 their long-term study of goshawks in Finland, Tornberg
 450 et al. (1999) suggested that big females that were effec-
 451 tive at capturing large prey (mountain hares) were likely
 452 selected for when grouse, the main prey for males, gradu-
 453 ally decreased and were replaced by smaller prey species.
 454 As we did not collect data on non-breeding adults, we can-
 455 not distinguish whether survival, acquisition of nesting ter-
 456 ritory or both processes are involved in the body size selec-
 457 tion, but we do not believe that body-size-mediated winter
 458 survival is relevant at our latitude (42°N). Winters in our
 459 study area are mild, with no frost or snow, in strong con-
 460 trast to the harsh winters of Finland, so a large size might
 461 not be crucial for maintaining body temperature. In addi-
 462 tion, the populations of several goshawk prey species arrive
 463 from the north, so no winter food limitation is expected

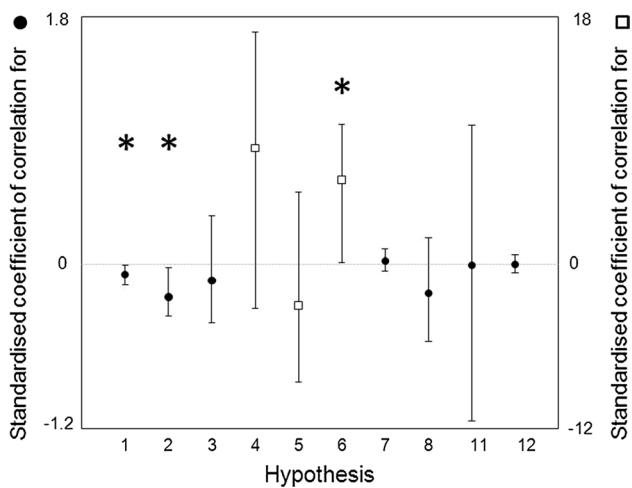


Fig. 1 Standardised coefficient of correlation ($\pm 95\%$ CI) of the GLMM for each hypothesis. Male body size in relation to (1) number of fledged young, (2) male body condition, (3) number of prey carried to the nest per day, (4) mean weight of prey, (5) percentage of forest prey, (6) percentage of non-forest prey. Female body size in relation to (7) number of fledged young, (8) female body condition. Male body size in relation to (11) female body size, and intrapair dimorphism index in relation to (12) number of fledged young. The alternative hypothesis can be accepted if the 95 % CI does not include zero, in which case the sign of the 95 % CI value indicates the sign of the relationship between variables. 95 % CIs that do not include zero are marked with *asterisk*. See also Tables 1 and 2

464 in our study area. These considerations lead us to suggest
 465 that acquisition of nesting territory is the primary pro-
 466 cess favouring larger females, as McDonald et al. (2005)
 467 pointed out for the Australian brown falcon (*Falco berigora*
 468 Vigors and Horsfield).

469 We hypothesise that two processes may favour larger
 470 females during acquisition of nesting territory: intersexual
 471 selection, in which males that hold a territory prefer to
 472 mate with the largest females; and intrasexual competition,
 473 in which females of different sizes compete for access to
 474 nesting territories (Olsen and Olsen 1987; Bortolotti and
 475 Iko 1992; McDonald et al. 2005). Since our results show
 476 that the highest-quality males (i.e. small males) did not
 477 mate with the largest females, we think that intrasexual
 478 competition among females for nesting territory may be the
 479 more important process. Consistent with this idea, the more
 480 dimorphic pairs in our study did not show greater reproduc-
 481 tive success than the less dimorphic ones. This may mean
 482 that larger females are at an advantage when attempting to
 483 acquire nesting territories but are not more productive than
 484 smaller females. As reviewed by Kenward (2006), less than
 485 8 % of the female fledglings in three different goshawk
 486 populations produced 50 % of the fledglings in subsequent
 487 years, suggesting that evolutionary changes in goshawk
 488 body size may occur very quickly if recruitment depends
 489 on this trait, as the present study suggests.

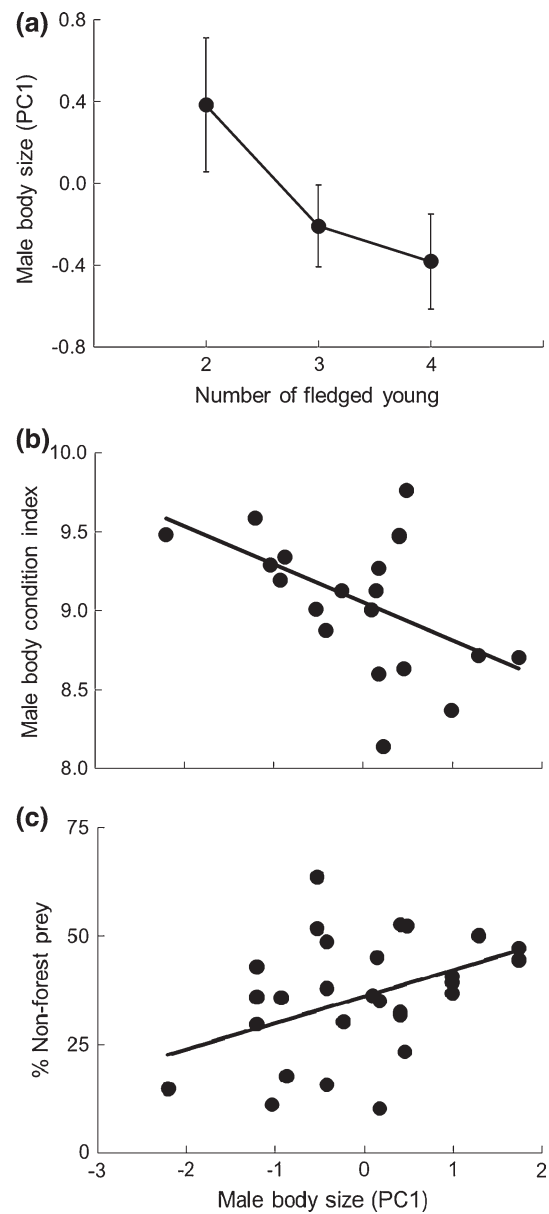


Fig. 2 Body size of male of goshawks in NW of Spain in relation to **a** number of fledged young, **b** body condition of males and **c** percentage of non-forest prey brought to the nest. Error bars indicate 1 SE

Further studies in which individually tagged birds of dif-
 490 ferent sizes are tracked until their first breeding are needed
 491 to demonstrate whether body size affects recruitment. In
 492 addition, research that takes into account the body sizes
 493 of both female and male goshawk fledglings, floaters and
 494 breeding individuals are needed to elucidate the individual
 495 contributions of survival and acquisition of nesting territory
 496 to RSD.
 497

Finally, our results reveal that body size can be used to
 498 assess the quality of individuals as future breeders, even as
 499 early as in the fledgling stage. The higher quality breeders
 500

Author Proof

Table 2 Results of study hypothesis testing

Hypothesis	Hypothesis is accepted?
Reproductive success hypotheses	
Nimble male hypothesis	
(1) Small males have greater reproductive success (more fledglings)	Yes
(2) Small males have better body condition	Yes
(3) Small males capture more prey	No
(4) Small males capture smaller prey	No
(5) Small males capture more forest prey	No
(6) Small males capture less non-forest prey	Yes
Big mother hypothesis	
(7) Large females have greater reproductive success (more fledglings)	No
(8) Large females have better body condition	No
Recruitment hypothesis	
(9) Small males have greater recruitment	No
(10) Large females have greater recruitment	Yes
Competition for mate hypothesis	
(11) Small males and large females tend to mate	No
(12) Couples formed by small males and large females have greater reproductive success (more fledglings)	No

Hypothesis 2–6 and 8 were assessed during the nestling phase

Table 3 Tarsus length (mean \pm SE), a surrogate for body size, for male and female fledglings and breeding adults

Sex	Tarsus length (mm)			<i>t</i>	<i>df</i>	<i>p</i>
	Fledglings	Breeding adults				
Males	74.07 \pm 1.54 (14)	74.28 \pm 2.40 (19)		0.28	31	0.78
Females	81.71 \pm 1.83 (17)	83.20 \pm 2.20 (20)		2.22	35	0.03

Sample numbers appear in brackets

t refers to the Student's *t* test statistic, *df* to the degrees of freedom

Values that are significantly different for fledglings and breeding adults ($p < 0.05$) are shown in bold

501 in our study were small males because of their higher
502 fledgling production, and possibly large females because of
503 their greater recruitment. These insights, if integrated into
504 local reintroduction programs, may be useful for popula-
505 tion management and species conservation.

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