Selection on body size in a raptor with pronounced reversed sexual size dimorphism: are bigger females better?

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An overabundance of hypotheses have been proposed to account for reversed sexual size dimorphism (RSD; females the larger sex) in raptors. Previous research principally focused on examining interspecific patterns of RSD, rarely testing predictions of various hypotheses within populations. To redress this, we used data from both sexes of a large brown falcon, Falco berigora, to evaluate the importance of size and body condition indices on the hunting prowess of males and the reproductive success, recruitment, and survival probabilities of both sexes. Female-female competition for territorial vacancies was likely to be intense as the floating population was female-biased and intrasexual agonistic interactions were frequently observed. In this competitive population, larger adult females were more likely to be recruited, indicating directional selection favoring increased female body size. Furthermore, after recruitment larger females were more likely to successfully fledge offspring, providing a mechanism by which RSD is maintained in the population. In contrast, male recruitment was unrelated to either body size or condition indices. Smaller immature males more often held their territories (survived) over two breeding seasons than did their larger counterparts; however, they also took small prey more frequently, a diet related to poor reproductive success. We argue that, together, these results are indicative of selection favoring an increase in female body size and a reduction or maintenance in male body size. Of all the hypotheses proposed to account for the maintenance and evolution of RSD in raptors, this scenario is consistent only with the predictions of the intrasexual competition hypothesis. Key words: body condition, Falco berigora, reversed sexual size dimorphism, size.

The evolution and maintenance of sexual size dimorphism in birds has long fascinated biologists, with Darwin (1871) himself writing on the subject in his pivotal treatise. In cases of nonreversed sexual size dimorphism (NRSD), in which the male is the larger sex, dimorphism has been attributed to sexual selection for larger male size and the competitive advantages this confers during competition for females (for review, see Andersson, 1994). Despite this, a consensus concerning the evolution and maintenance of reversed sexual size dimorphism (RSD), in which females are the larger sex, has yet to be reached. Indeed, for the typically RSD raptors, comprised of the Falconiformes and Strigiformes, well over 20 hypotheses have been proposed (see Amadon, 1959, 1975; Andersson, 1994; Andersson and Norberg, 1981; Earhart and Johnson, 1970; Jehl and Murray, 1986; Lundberg, 1986; Mueller, 1986, 1990; Mueller and Meyer, 1985; Newton, 1979; Simmons, 2000; Snyder and Wiley, 1976).

Despite this, predictions arising from hypotheses have rarely been rigorously tested, particularly in intraspecific studies. Most hypotheses proposed have been based on generalizations from secondary data sources using comparative analyses. In these analyses, simple single measures of body size have usually been used, with samples often separated both temporally and spatially within/between species assessed in comparisons. Unless these single structures are important in maintaining RSD, they provide limited predictive power (McGillivray, 1985). A better approach may be to use principal component analyses (PCAs) to generate overall estimates of size spread across several measures, keeping body mass separate to avoid biasing the PCA (Alisauskas and Ankey, 1990; Freeman and Jackson, 1990; Rising and Somers, 1989). Moreover, hypotheses proposed to account for RSD should have general application (Jehl and Murray, 1986) and be able to explain both the direction and degree of the dimorphism (Olsen and Cockburn, 1993), preferably in more than one group, a feature lacking in many hypotheses proposed to account for RSD in raptors.

In a bid to address the general lack of, and many cases limitations of, existing data in this field, we investigated the direction of selection upon body size in both sexes of a large population of color-banded Australian brown falcons, Falco berigora. In turn, this information was then used to assess the relevance and broad applicability of the various hypotheses proposed to account for RSD in raptors.

METHODS

Study area, species, and general field methods

The brown falcon is a moderately dimorphic raptor (mean ± SE, males: 486 g ± 5, wing length = 331 mm ± 1, n = 69; females: 658 g ± 7, wing length = 361 mm ± 0.9, n = 91; McDonald PG, unpublished data) common across most of Australia, present in virtually all habitats except closed forest. Pairs of falcons maintain all-purpose territories throughout the year, have a high mate fidelity, and are long-lived, with some individuals still breeding at 18 years of age (McDonald, 2003b, 2004; McDonald et al., 2003). Brown falcons do not build their own nests, instead they appropriate an open stick nest, usually that of a corvid (McDonald et al., 2003). This study was conducted between July 1999 and June 2002, approximately 35 km southwest of Melbourne in southeastern Australia, at the Western Treatment Plant (WTP), Werribee (38°0′ S, 144°34′ E), adjacent Avalon Airport (38°2′ S, 144°28′ E) and small areas of surrounding private land.
Details of the study site have been described elsewhere (Baker-Gabb, 1984), as has the study population (McDonald, 2003a,b, 2004; McDonald et al., 2003, 2004).

Body size indices

Falcons were captured with bal-chatri and modified goshawk traps (Bloom, 1987) on their territories from approximately June through the following January each season and fitted with a unique combination of color bands and a metal service band, before being released at the point of capture. Before release flattened wing chord, tail length, exposed culmen, head-to-bill length, and body mass measures were taken.

The diet of each pair, and thus falcon, was determined by using the methods of McDonald et al. (2003). Briefly, all prey taken fell into five distinct groups: lagomorphs, nonpasserines, large reptiles, small ground prey (insects/rodents), and small passerines according to the prevailing land-use regime of each territory (McDonald et al., 2005). Each pair took the majority of prey items (in terms of numbers not biomass) from one of these five prey groups for simplicity these groups were further reduced to pairs taking large prey (lagomorphs, nonpasserines, large reptiles) and those taking small prey (passerines and ground prey). Many pairs took prey from one of these size classes exclusively; however, in some cases pairs scored as taking large prey occasionally took a minority of prey items from the small prey category and vice versa (see McDonald et al., 2003). Throughout, the probability of taking large prey refers to the probability of a given pair being classified as predominantly taking large, as opposed to small, prey overall. Large prey items were mainly juvenile rabbits, Oryctolagus cuniculus, along with nonpasserines and elapid snakes, with a mean geometric prey mass of 155 g, whereas small prey items weighed 59 g and were usually rodents, invertebrates, or small passerines (McDonald et al., 2003). Each prey size was present in different concentrations on each territory, and although the biomass of each was not sampled on each territory, smaller prey were not delivered to nests at a significantly greater rate than were large prey (McDonald, 2004). This indicates fewer resources were available for breeding and likely subsistence among pairs taking small prey.

Captured falcons were classified as possessing either adult (acquired at 4–6 years old) or immature plumage (birds range from 2–4 years old) based on banding records or plumage characteristics (McDonald, 2003b; Weatherly et al., 1985). Juveniles less than 2 years of age were excluded from analyses. The bare parts (orbital ring and cere) and front plumage of adults and immatures were scored for relative brightness on each territory, female making numerous swoops flushing, before flying from view; 2, when flushed female stayed within 50 m and within view of the nest site; 3, both sexes attended nest area, female making numerous swoops within 3 m of climber; 4, both sexes swooping within 3 m of climber; and 5, physical contact made with climber by defending female.

Recruitment

The identity of all banded falcons holding territories was established each year of the study, allowing survival from one postbreeding season to the following prebreeding season to be assessed. Each individual was also scored as either obtaining a territory in the year of capture or remaining part of the unsuccessful floating population. Individuals no longer on the study site were presumed to have died, although a small degree of emigration is possible (McDonald et al., 2003). The number of breeding seasons individuals remained on the study site (tenure) was also determined from these data.

Reproductive parameters

During each breeding season, all nests within the study area were found and their contents determined by visiting the nest or using a mirror pole. Length and breadth of eggs were measured to the nearest 0.01 cm with vernier calipers at the longest and widest point, respectively. Egg volume was estimated by using the formula: 0.51 × length × (breadth)² (Hoyt, 1979); once clutches were complete, mean egg volume was determined for each clutch. If not observed directly, laying date of the first egg for each clutch, hereafter “lay date,” was estimated by using the methods outlined in McDonald et al. (2003). When clutches were close to hatching, nests were visited regularly to determine the number of eggs successfully hatched, that is, brood size. After hatching, nests were visited weekly to determine the number of offspring fledged and thus if the breeding attempt was successful (fledged at least one offspring). To correctly assign sex to each nestling, molecular methods were used (polymerase chain reaction/HaeIII digest; Griffiths et al., 1998). Chicks were marked at hatching and banded at approximately 28 days of age. Sex ratios of broods were determined at both hatching and fledging.

Nest defense

The responses of each pair to nest visits were recorded during the 2000 and 2001 breeding seasons. As the population is largely free of nest predators, human persecution is likely to be the only significant form of predation (McDonald et al., 2003). During each nest, visit P.M. scored the parents response as one of the following: 0, female flushed from nest and silently flew from view; 1, female called briefly after flushing, before flying from view; 2, when flushed female stayed within 50 m and within view of the nest site; 3, both sexes attended nest area, female making numerous swoops within 3 m of climber; 4, both sexes swooping within 3 m of climber; and 5, physical contact made with climber by defending female.

Male provisioning rate

During the breeding seasons of 2000 and 2001, intensive assessments of prey deliveries by known (banded) males to nests were conducted by using surveillance cameras (model 43150674; Radio Parts Group) placed at nests for 48-h periods throughout the nestling phase. Cameras were powered by deep cycle batteries (Besco N70T; Battery World) and connected to time-lapse video recorders (Hitachi VT1200E;
Radio Parts Group) run at a one-eighth normal speed. This setup reduced visits to the nest area to 24-h intervals to change batteries and tapes. As females began to hunt by the time the eldest chick was 3–4 weeks old (McDonald, 2004), analyses of prey delivery were confined to the early (eldest chick, 0–14) and mid nestling phases (eldest chick, 14–28 days old) when males provided the bulk of prey items. The number and identity of prey delivered by males to each nest was subsequently identified from video footage. Each item was then assigned a mean weight from the method of McDonald et al. (2003), and the total biomass delivered per 48 h by each male was calculated and used as an estimate of male quality.

Statistical analyses

Generalized linear models with binomial error distributions (Genstat Committee, 1993) were used to assess relationships between size variables (structure, feather, and condition) and binomial estimates of fitness in the year of capture, such as the probability of a bird attempting to breed and being successful once breeding was initiated, and the probability of a female successfully hatching a given egg or fledging a nestling. Generalized linear models were used to assess the impacts of size upon tenure and continuous measures of reproductive success such as lay date and mean egg volume. As mean egg volume was not measured in all years of the study, the first clutch measured from a given female was compared to structure scores only (fixed in immature and adult birds), regardless of the year of capture. Previous research has determined that both the mortality and reproductive success of this species is influenced by factors other than body size, in particular climatic conditions and age (McDonald et al., 2004). To account for this, year of capture was included as a variable in models, and both ages of each sex were analyzed separately. Year was not a significant factor in any analysis reported, and thus for simplicity, statistics for this variable are not presented.

We used restricted maximum likelihood (REML) procedures to account for size influences on nest defense and male prey delivery rates. When analyzing nest defense scores, we included a random model with female and nest number, with the main model including Julian nest visit date, the number of previous nest visits, nest stage (incubation; early, mid, or late nestling phase), and whether either sex had experienced human interference in previous years.

A total of 387 prey deliveries by males were recorded, accounting for 57.7 kg of prey mass. A minority (4.9%) of prey items were obscured from the camera, preventing identification; linear regressions predicting prey mass from the number of mouthfuls given to chicks at each age (early or mid nestling phase) were constructed to generate mass estimates of these items. Regressions explained 42.3% (early; \( F_{1,200} = 146.7, p < .05, \text{biomass } [g] = 13.5 \text{ [feed duration, min] +9.7} \)) and 52.9% (mid nestling phase; \( F_{1,102} = 182.0, p < .05, \text{biomass } [g] = 20.8 \text{ [feed duration, min] +26.9} \)) of variation in prey weight. The total biomass delivered by males per 48 h was then calculated and normalized with a square root transformation \( X' = [X + 0.5]^{1/2} \) (Zar, 1996) before being subjected to a REML analysis. The random model used included the variables pair, male number (randomly assigned), and the number of times focal males had been observed in each breeding season. In addition to size variables of both sexes, the main model included the terms brood reduction (death of at least one nestling), year, chick age (early or mid nestling phase), brood size, lay date, prey size, brood sex ratio at hatching, and experience (number of years pair known to have bred together).

RESULTS

Recruitment, tenure, and survival

Adult females with a larger structure score were more likely to hold a territory in the year of capture (Figure 1 and Table 1). However, as some individuals sampled may have inherited uncontested territories, we also investigated the relationship between structure and the probability of gaining immediate recruitment into the breeding population (instant recruits) as opposed to those females that spent time as part of the floating population. Adult female instant recruits \( (n = 4) \) again had larger structure scores (Figure 2) than did other recruited females \( (n = 3; R^2 = .5, F_{1,6} = 9.5, p = .02) \). Recruitment of immature females and both age groups of males was not influenced by size or body condition indices (Table 1).

The length of tenure was not influenced by structure, feather, or body condition scores among any sex or age group (Table 1). The same was true for the probability of survival to the next breeding season, with the exception of immature males (Table 1). Immature males with a larger structure score had a reduced probability of survival to the next breeding season (Figure 3a and Table 1).

Mate/territory quality and the likelihood of breeding

Body size or condition indices were not related to the probability of either age or sex group obtaining an adult
Table 1
Summary of factors influencing demographic and reproductive parameters of brown falcons of different sex and age groups

<table>
<thead>
<tr>
<th>Parameter examined</th>
<th>Adult females</th>
<th>Adult males</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>S</td>
<td>F</td>
</tr>
<tr>
<td>Probability of recruitment</td>
<td>7.3** (48)</td>
<td>2.9 (48)</td>
</tr>
<tr>
<td>Tenure</td>
<td>$F_{1,42} = 0.01 (43)$</td>
<td>$F_{1,44} = 0.5 (43)$</td>
</tr>
<tr>
<td>Probability of survival</td>
<td>0.5 (44)</td>
<td>1.0 (44)</td>
</tr>
<tr>
<td>Probability Adult partner</td>
<td>0.3 (44)</td>
<td>0.2 (44)</td>
</tr>
<tr>
<td>Probability of taking large prey</td>
<td>0.01 (44)</td>
<td>1.2 (44)</td>
</tr>
<tr>
<td>Attempt to breed</td>
<td>3.2 (44)</td>
<td>0.01 (44)</td>
</tr>
</tbody>
</table>

Data modeled by using general linear models with binominal distributions, except in the case of tenure, in which a general linear model was used. Figures indicate change of deviance statistics associated with structure (S), feather (F), and body condition indices (C) and approximate a chi-squared distribution with one degree of freedom unless noted otherwise. Numbers in brackets indicate sample sizes. As all but one of the adult males sampled were recruited, analysis of the influence of adult male size on the probability of successful recruitment was not possible. * $p < .05$, ** $p < .01$, significant ($p < .05$) figures and associated parameter terms are emboldened.

Breeding success

Low sample sizes of successful birds prevented an analysis of the effect of body size upon the productivity of breeding attempts by immature falcons. Adult females with a larger feather score were more likely to be classified as predominantly taking large prey items (Figure 3b and Table 1). However for adult males and both ages of females, no relationships between body size or condition indices and prey preference were apparent (Table 1).

Male hunting prowess

The amount of prey delivered to nests by males was not related to their own body size or condition index, or that of their partner (Table 4). Instead, males with brighter, completely yellow bare parts delivered significantly more prey (1.8 kg $\pm$ 0.2; $n = 17$) in 48 h than did those with only partially yellow bare parts (1.2 kg $\pm$ 0.2, $n = 20$) (Table 4). More importantly, males taking larger prey items delivered 1.8 kg ($\pm$ 0.2, $n = 22$) of prey to their nests per 48 h, almost twice that supplied by males taking small prey (1 kg $\pm$ 0.1, $n = 19$) (Table 4).

DISCUSSION

Adult females in the study population with larger skeletal measures had a higher probability of obtaining a territory in the study site than did their smaller counterparts. Moreover, once recruited, adult females with larger feather scores (wing/tail lengths) were more often successful in their breeding attempt and had a greater probability of fledging a given nesting within their brood. In contrast, adult male recruitment was unrelated to body size or condition indices; however, fatter males were more productive, having a greater chance of fledging their nestlings and pairing with partners that initiated clutches earlier in the season. Immature male falcons with smaller structure scores were more likely to survive to the next breeding season, but paradoxically, were less likely to be taking large prey items, a better prey resource. Thus, directional selection on body size appears to be favoring large size among adult females and a reduction or stabiliza-
birds captured and also within the subgroup bypassing the floating population. Further, the greater breeding success of individuals with large feather scores provides a mechanism by which RSD could be maintained in the population. Females were more prevalent in the floating population than were males (McDonald PG, unpublished data), which, along with frequent female-female agonistic interactions (McDonald, 2004), indicates strong female competition for access to vacancies in the breeding population. Strong female intra-sexual competition has been noted in other raptor species (Newton, 1986, 1988; Simmons, 2000; Temeles, 1986), and larger body size is thought to be important in intraspecific disputes (Hansen, 1986; Knight and Skagen, 1988).

Despite their apparent competitive superiority, larger females did not choose higher-quality mates or territories. Although it is possible females were competing over a factor not sampled in this study, high population density appears a more likely explanation for this apparent lack of mate choice. The population studied is the densest recorded for this species (McDonald et al., 2003). Given territory fidelity is high and both sexes defend territories from intruders of either sex (McDonald, 2004), female mate choice may be limited by a high probability of being usurped. Moreover,
Despite male condition being an important indicator of quality, no evidence of competition between females for fatter males was found (McDonald PG, unpublished data).

In contrast to females, male body size was not an important determinant of recruitment among either age group or the productivity of adult falcons. Instead, adult males with higher indices of body condition bred earlier and, perhaps as a consequence, had a greater probability of fledging nestlings within their brood. Nevertheless, at least within those males sampled, fatter falcons were not supplying their brood and partner with a greater biomass of prey. Instead, bare part coloration and prey size were important indicators of prey delivery rates, both factors females could potentially assess directly if the opportunity for mate choice arose.

Survival patterns indicated directional selection favoring small immature males, which were more likely to capture small prey (McDonald et al., 2004). Superficially, this result appears to support the idea of intersexual niche differentiation RSD hypotheses that predict a reduction in male size and male’s prey (see Storer, 1966). However, body size was not an important determinant of prey choice among adult males or females of any age. Moreover, both sexes of brown falcons within pairs take similar prey items, with the largest and smallest birds alike (either within or between sexes) being able to capture both the smallest and largest prey items recorded (McDonald et al., 2003).

One possible explanation of these effects is intrasexual competition, as larger immature male falcons were occupying territories conducive to the capture of preferred large prey they may have been more likely to be replaced by competitively superior males (e.g., adults), leading to greater apparent mortality rates. Alternatively, large prey such as eastern tiger snakes, *Notechis scutatus*, and rabbits are likely to be far more dangerous and difficult to capture than are smaller prey items, particularly for relatively inexperienced immatures. Hunting accidents may therefore also increase mortality amongst larger immature males.

**Implications for hypotheses proposed to account for RSD**

First, behavioral hypotheses argue larger female raptors are better able to force smaller males into pairing, provisioning them or their offspring or preventing male infanticide (Amadon, 1975; Cade, 1982; Mueller, 1986, 1990; Mueller and Myer, 1985; Smith, 1982). These hypotheses lack universal application, cannot predict the direction of dimorphism, and are severely compromised by the existence of NRSD species with similar life-history strategies (e.g., some *Ninox* owls; Higgins, 1999; Olsen and Cockburn, 1993; Olsen and Olsen, 1987; Schodde and Mason, 1980). Brown falcon pairs with
lager females did not begin laying earlier and male infanticide was not recorded in the population, despite some males providing food to nests in the absence of females and even feeding nestlings (McDonald, 2004).

Second, ecological hypotheses suggest that RSD has evolved to reduce intersexual and/or intrapair competition for food (see Selander, 1966; Snyder and Wiley, 1976; Storer, 1966). These hypotheses have drawn many criticisms (for review, see Olsen and Cockburn, 1993), chief among which is the failure to explain the presence of RSD in species in which the sexes spend little time together (Myers, 1981; Newton, 1979) and the scant evidence of significant sexual resource partitioning (Mueller, 1990), which was also not evident in the study population (McDonald et al., 2003). A much stronger relationship exists between the agility of prey and the degree of RSD (Newton, 1979; Simmons, 2000; Temeles, 1985); this is usually argued, but not yet demonstrated, to have occurred through a reduction in male size favoring the capture of more agile prey (see Newton, 1979; Temeles, 1985). No support for this hypothesis was found for brown falcons: there was no relationship between prey agility and the degree of RSD (Newton, 1979; Simmons, 2000; Temeles, 1985); this is a consequence of recruitment favoring increasing female size, and thus RSD, than the principal factor facilitating more successful brooding of young by female brown falcons during inclement weather is more likely to be driven by natural selection.

Third, sex role differentiation hypotheses focus on the distinct parental roles evident in raptors. They argue that smaller males have been favored for their greater foraging efficiency or superior territorial defense, whereas larger female size allows more effective incubation, larger egg/clutch sizes, and/or better nest defense (Balgooyen, 1976; Hakkarainen and Korpimäki, 1991, 1995; Hakkarainen et al., 1996; Lundberg, 1986; Reynolds, 1972; Selander, 1972). Clearly the intensity of nest defense by brown falcons was unrelated to body size in either sex, and this, along with the fact that small males are the main defender of nest sites in many other raptors exhibiting marked RSD (Andersson and Wiklund, 1987; Simmons, 2000; Wiklund and Stigh, 1983), indicates nest defense is unlikely to influence the maintenance or evolution of RSD in raptor populations. Prey delivery rates by male brown falcons were also unrelated to body size, indicating smaller males were not more effective hunters. Further, larger female brown falcons did not hatch a greater proportion of their eggs or lay larger eggs, indicating increased egg volume is also not likely to be a significant influence upon RSD in raptors.

Despite this, female brown falcons with larger feather scores were more likely to fledge nestlings within their brood and had a greater chance of reproductive success, providing some support for the hypothesis that larger female size has evolved to improve a females brooding ability (see Snyder and Wiley, 1976). However, this hypothesis is not likely to provide a general explanation for the existence of RSD in raptors as it cannot explain the degree of dimorphism evident between raptor species, the existence of both RSD and NRSD in species such as the Ninox owl genus, and the lack of RSD in many other bird groups. A possible role of larger feathers in facilitating more successful brooding of young by female brown falcons during inclement weather is more likely to be a consequence of recruitment favoring increasing female structure size, and thus RSD, than the principal factor responsible for the evolution of RSD.

Fourth, hypotheses centered around the effects of sexual selection can be divided into two types: those that suggest RSD is maintained by (1) intersexual selection in which females select smaller, more agile males that are capable of performing more attractive display flights and are better hunters (Hakkarainen and Korpimäki, 1991, 1995; Hakkarainen et al., 1996; Jehl and Murray, 1986; Safina, 1984; Simmons, 2000; Widén, 1984); and (2) intrasexual selection that favors an increase in size of females that compete for a scarce resource, a male holding a territory that is ready to breed (Olsen and Olsen, 1984, 1987). This hypothesis posits that male size is driven by natural selection.
The results from the present study have demonstrated that smaller male brown falcons were not more successful hunters. Moreover, neither size nor condition-mediated assortative mating, with larger females favoring smaller males, was apparent within the population (McDonald PG, unpublished data), indicating mate choice was not a primary factor in determining settlement patterns and thus RSD. Most other studies have also failed to find a female preference for small males in field-based assessments (Bowman, 1987; Marti, 1990; Palokangs et al., 1992; Warkentin et al., 1992). Together, these results suggest that the intersexual selection hypothesis does not appear likely to be a significant factor in maintaining RSD.

In contrast, the results gathered in the present study provide clear support for the intrasexual competition hypothesis (Olsen and Olsen, 1984, 1987), as larger females were more effective competitors for access to breeding territories and thus operational males; increased mortality of larger immature males and greater breeding success of larger females would maintain RSD. Some (see Andersson, 1994) have refuted the intrasexual competition hypothesis, citing the results of Wiklund and Village (1999), who examined sexual differences in the intensity of responses to simulated territorial intrusions, yet this study did not account for the relative body size of territory owners compared with intruders, a critical component of the intrasexual competition hypothesis. Massemin et al. (2000) examined selection pressure in common kestrels, failing to find strong directional selection in either sex (as expected in this species with limited dimorphism), but their study did not assess recruitment patterns, the period when larger female size is likely to be of most benefit. Searching for benefits of increased female size in reproductive success alone cannot be considered a conclusive test of the intrasexual selection hypothesis.

In contrast to many other proposed RSD hypotheses, the intrasexual competition hypothesis also has application to other bird species, including raptors with NRSD (e.g., Ninox owls; Olsen, 1991). It also accords well with current understanding of sexual selection, which is largely based on sex differences in parental investment that result in one sex becoming limited and the other competitive (Kokko and Johnstone, 2002; Kokko and Monaghan, 2001). In addition, this hypothesis can predict the degree of RSD in a species: dimorphism increases as the importance of securing a high-quality mate becomes more critical, for example, in species taking prey difficult to capture, accounting for the strong relationship between prey agility and RSD in many raptors (Olsen and Olsen, 1987).

In summary, the results of the present study, based on intensive sampling of large numbers of both sexes of the population, clearly support selection favoring an increase in female size and thus the predictions of the intrasexual competition hypothesis.

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