



Compensatory responses differ between parental tasks in a songbird species

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In species with biparental care, the amount of care devoted to offspring is affected by the negotiation rules that the parents adopt. Theoretical models predict that biparental care can be evolutionarily stable if a decrease in parental investment by one parent is only partially compensated by its partner. However, empirical studies have found substantial variability in compensatory behaviour and have mainly used nesting provisioning as a single measure of parental effort. In this study, we investigated parental compensatory behaviour for two parental tasks, offspring provisioning and nest defence. These two tasks are likely characterized by different levels of risk as well as different cost and benefit functions for the parents, which may affect the expected level of compensatory responses. We experimentally widowed (by temporarily removing one parent) male or female Spanish sparrows, *Passer hispaniolensis*, and measured their compensatory responses to offspring provisioning and nest defence (after predator presentation of green whip snake, *Hierophis viridiflavus*, models). Parents differed in their compensatory responses in relation to parental task and sex: both sexes partially compensated for offspring provisioning, but females compensated by a larger degree than males. For predator defence, males instead decreased defence behaviour by increasing latency and reducing the number of attacks, while females did not change their behaviour when caring alone. This within-individual comparison indicates that parents adjust their compensatory behaviour according to parental task. We discuss how these differences could arise due to different costs and benefits of extra investments.

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Parents often invest heavily in their offspring (Royle et al., 2012). In species with biparental care, parental allocation decisions not only depend on the trade-off between current and future reproduction for each individual (Roff, 2002; Williams, 1966) but are also affected by an evolutionary conflict of interest ('sexual conflict') between the two parents (Trivers, 1972). This conflict arises because costs and benefits of parental care investment are not equally shared between the two sexes: each parent benefits from the pair's total level of investment, while the cost of care is paid individually (Lessells, 2006). The inevitable consequence is that each parent is selected to exploit its mate by providing a smaller share of the care (Lessells, 2006). A central goal in evolutionary biology is to understand how sexual conflict ultimately modulates how much care parents of the two sexes are expected to provide to their offspring.

How sexual conflict is resolved evolutionarily has been the topic of extensive theoretical work. While an early model, proposed by Houston and Davies (1985), assumed that each parent makes an independent single decision about its parental investment that can change over evolutionary timescales, later models have included a negotiation phase in which each parent can behaviourally adjust ('negotiate') its level of investment in relation to that of its mate during each reproductive event (Johnstone & Hinde, 2006; Lessells & McNamara, 2012; McNamara et al., 1999, 2003). A major prediction of these models is that biparental care can be an evolutionarily stable strategy only if a decrease in care by one parent selects for a partial compensation by the other parent (McNamara et al., 1999, 2003). In other words, if one parent reduces its parental care allocation during a reproductive event, the partner should, on a behavioural timescale, increase its parental effort to a smaller magnitude, because a full compensation at no cost for the offspring would leave the caring parent open to exploitation by the partner, who would benefit to further reduce its contribution to zero (Houston et al., 2005).

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The theoretical prediction of partial compensation has been empirically studied on a wide range of taxa, such as insects (Donaldson et al., 2013; Rauter & Moore, 2004; Smiseth et al., 2005; Suzuki & Nagano, 2009), fish (Lavery & Reeb, 1994; Mrowka, 1982; van Breukelen & Itzkowitz, 2011) and birds (Griggio & Pilastro, 2007; Schwagmeyer et al., 2008; reviewed in Harrison et al., 2009). These studies adopted experimental approaches in which one parent was either temporarily removed (Cantarero et al., 2019; Iserbyt et al., 2019; Mainwaring & Hartley, 2020; Suzuki & Nagano, 2009; van Breukelen & Itzkowitz, 2011) or manipulated to reduce its parental effort, e.g. via handicapping (Griggio et al., 2005; Sanz et al., 2000), hormone treatment (Schwagmeyer et al., 2008; Van Roo, 2004), ornament treatment (Qvarnstrom, 1999) or selective playback of begging signals (Hinde, 2006; Hinde & Kilner, 2007; Ottosson et al., 1997). Although the results of these experiments were generally in line with the theoretical prediction of partial compensation, as suggested by a meta-analysis of studies in birds (Harrison et al., 2009), there was nevertheless substantial variation in compensatory behaviour (Lessells, 2012), with responses including matching (Hinde, 2006; Hinde & Kilner, 2007) and complete compensation, no compensation (Bowman & Bird, 1987) or even overcompensation (Griggio & Pilastro, 2007; Royle et al., 2002).

Currently, the deviation between the initial theoretical predictions and the observed compensatory responses (both in terms of direction and magnitude of the response) in the experimental studies has received two different interpretations. One explanation is that the parental effort of one individual also conveys information to its partner about the current brood 'value' or 'need', leading to different expected levels of compensatory responses (Johnstone & Hinde, 2006). The second explanation entails the potential temporal lag between the observed parental responses and the type of manipulation performed (Mainwaring & Hartley, 2020; Suzuki & Nagano, 2009). Specifically, responses to a partner's reduction in parental care allocation were not found immediately after manipulation but emerged at later stages, suggesting a delayed response to the partner's parental allocation (Mainwaring & Hartley, 2020). Mate removal experiments produced a stronger response compared to mate handicapping ones (Harrison et al., 2009; Suzuki & Nagano, 2009). Another reason for the disparity of results is that previous studies have focused on a single parental care behaviour, typically chick provisioning, as a proxy for parental compensatory effort and have almost entirely neglected other parental tasks, such as predatory defence, with the exception of a few studies (Sowersby et al., 2017, 2018; Trnka & Grim, 2012; van Breukelen & Itzkowitz, 2011). For instance, Trnka and Grim (2012) tested the partial compensation hypothesis in the context of nest defence in a passerine species, the great reed warbler, *Acrocephalus arundinaceus*, and found no compensation and even reduced parental investment when one parent was protecting the offspring alone. These results suggest that the expected outcome of compensatory responses might also vary among parental tasks, especially if different parental duties are characterized by different benefit functions to the offspring and different cost functions (e.g. immediate mortality risk associated with defence against predators versus future mortality risk associated with feeding effort) for the parents (Montgomerie & Weatherhead, 1988; Regelman & Curio, 1986). Presently, the lack of an integrated compensatory theory that considers different parental tasks and the paucity of empirical investigations that consider more than a single component of parental effort at the same time (typically feeding effort) may hinder our understanding of the negotiation rules that parents adopt when caring for offspring.

In this study, we used a breeding population of Spanish sparrow, *Passer hispaniolensis*, and applied a within-individual design to

experimentally test parental compensatory responses to short-term partner removal on two concomitant parental tasks: offspring provisioning and predator defence. In birds, both male and female parents usually contribute to chick feeding and defence (Montgomerie & Weatherhead, 1988; Nakagawa et al., 2007; Redondo, 1989; Westneat et al., 2011), although among-species variation exists regarding sex roles (Balshine, 2012; Cockburn, 2006), with a bias towards more female care (Cockburn, 2006). Furthermore, there is evidence that coordinated provisioning and joint defence behaviour between parents increases reproductive success and reduces nest predation risk (Bebbington & Hatchwell, 2016; Burtka & Grindstaff, 2015; Speelman et al., 2022). The aim of this study was to evaluate whether compensatory responses differ between parental tasks and whether this could be due to differences in cost and benefit functions associated with these tasks. Here we assumed that chick provisioning and predator defence behaviours are defined by two distinctive cost and benefit functions. Specifically, for chick provisioning behaviour, we assumed that the benefit would increase with diminishing returns as provisioning visits increased. For provisioning, we expected that the benefit would be bounded by an upper limit, where offspring would be satiated and would not increase the rate of energy assimilation provided by extra food on a short timescale (Karasov & Carey, 1996). The cost of provisioning is expected to increase non-linearly with the number of provisioning visits, due to the accumulation of physiological costs (Alonso-Alvarez & Velando, 2012; Williams, 2018). For predator defence behaviour, such as mobbing by the parents towards a predator, we assumed that the benefit would increase linearly with the number of attacks, as each single attack has an individual and independent probability to deter the predator until the predator has been successfully chased away, and therefore, the probability to deter the predator increases with attack intensity (i.e. the frequency of attacks in a given time). However, once the predator is driven off, additional attacks would provide no further benefits for the parents or the offspring. As for provisioning behaviour, we assumed the cost of defence would increase with the number of attacks because of the associated physiological costs of intense mobbing and its associated risk for the adults to be captured or wounded by the predator. Based on differences in how benefits accumulate over time between the two parental behaviours, we predicted that, following mate removals, the remaining parent would only partially compensate its provisioning visits to the offspring, due to the diminishing returns of extra feedings. For predator defence, we predicted that parents would show a stronger compensatory response because the benefits of defence per single attack is constant or even increasing, and there would be a higher level of compensation (possibly full compensation) than for chick provisioning.

METHODS

Study Species

The Spanish sparrow is a small passerine species belonging to the genus *Passer* (Gill et al., 2022). Similarly to the house sparrow, *Passer domesticus*, the Spanish sparrow is sexually dimorphic and males are characterized by a black bib and black streaks that extends to the lower chest and sides. Its geographical distribution includes the Mediterranean basin (Gill et al., 2022) and, during the reproductive season, the Spanish sparrow forms large reproductive colonies (Roviralta, 2016). In this species, parental care is biparental and adults typically breeds over consecutive years with a different mate (M. Griggio, personal observations). Because monogamy across years is rare, each single breeding attempt is likely to be under strong selection for exploitation of parental effort by the

partner (Griffith, 2019; Johnstone & Savage, 2019) and, therefore, we expected compensatory responses to mate removal to be conserved. During the chick provisioning period, both male and female parents frequently feed their offspring at the nest with grasshoppers or caterpillars found when foraging in the nearby area (Marques, 2004), and nest defence from terrestrial predators (i.e. snakes) involves alarm and contact calls produced by both parents followed by flight incursions and direct attacks towards the predator (M. Griggio, personal observations).

Study Area

We conducted our study on a breeding population of Spanish sparrow in Sardinia, Italy (40°23'30"N, 9°12'12"E). This area is situated in a woodland dominated by cork oaks, *Quercus suber*, and contained 45 nestboxes established in 2008. These boxes are occupied every year by breeding pairs of Spanish sparrows and rock sparrows, *Petronia petronia* (Baldan & Griggio, 2019). Each year, we checked the nestboxes every 2 days from the beginning of May until the fledging of the last chicks (July). For each active nest, we monitored the date of the first laid egg, hatching date, clutch and brood size and fledgling success. We also trapped the adults at the nest during the chick provisioning period to measure body mass (to the nearest 0.1 g) and tarsus length (to the nearest 0.1 mm) and marked each parent with a metal ring and a unique combination of coloured rings. In this population, the main nest predators are green whip snakes, *Hierophis viridiflavus*, which are relatively abundant in this area (M. Griggio, personal observations).

Experimental Set-up

We carried out our experiment over four consecutive breeding seasons, from 2015 to 2018. Every year, we randomly allocated Spanish sparrow nests to three different experimental groups: a control group, a male-removed and a female-removed group. For each experimental nest, our experimental set-up consisted in a preremoval phase and a postremoval phase. In the preremoval phase, we observed the nest for 1 h in the morning with a 20 × 60 spotting scope while sitting in the open, approximately 30–50 m from the nest. We observed parental provisioning behaviour and, for each parental visit at the nest, we noted the identity of the parent. In all the provisioning visits, we observed the parent bringing food to the nests. At the end of the preremoval phase, we caught one parent in the male- and female-removed group in a trap placed inside the nestbox. The sex of the removed parent was randomly predetermined, and the nest trap was designed with a transparent fishing line so that the operator could selectively close the trap to capture the experimental subjects. In the control group, we visited the nestbox at the end of the preremoval phase, but we did not catch any parent. We placed the caught individual inside a cotton bag until the end of the postremoval phase and predator presentation. One hour after the capture of one parent, we carried out another 1 h observation, similarly to the preremoval phase, in which we observed the provisioning behaviour of the remaining parent (focal parent, postremoval phase). After the 1 h observation period, we placed a plastic snake model on the roof of the nestbox to quantify the parental antipredator behaviour of the pair (for the control group) or of the focal parent (for the male- and female-removed groups). We used two predator models, that had the same dimensions and similar coloration of the snakes present in the study area (*H. viridiflavus*) and were randomly rotated across the experimental nests. We placed the predator at the nest within 1 min without being seen by the parent(s). We did this soon after the focal parent(s) left the nest to forage, and we never heard alarm calls from the parent(s) directed towards us, suggesting that our

experimental intervention passed unnoticed. Once we placed the predator model on the nestbox, we recorded the 'latency' for the focal parent(s) to respond as the time (in seconds) taken by the focal parent(s) to arrive at the vicinity of the nest, as in Trnka and Grim (2012). We considered latency to be a negative proxy for the parents' nest defence (e.g. a higher nest defence denotes a shorter latency to detect and respond to predators; Trnka & Grim, 2012), and it is assumed to be traded off with provisioning behaviour, because during nest defence, parents must restrict their foraging to the vicinity of the nest and potentially miss out on other foraging opportunities (Komdeur & Kats, 1999). Once the focal parent was seen at the nest site, we counted the number of attacks by the bird to the predator model for the next 5 min. We defined an attack as a direct flight towards the model that resulted in an approach <2 m or body contact (Mahr et al., 2015; Matessi et al., 2009). At the end of the 5 min predator presentation, we removed the dummy predator and released the captured parent. The captured parent was always seen feeding the offspring at the nest within a couple of hours from the release. For each nest, the experiment started at 0800 hours and ended by 1130 hours when chicks were between 11 and 13 days old (hatching day = day 0). In total, we carried out our experiment on 75 pairs: 26 control, 28 female-removed and 21 male-removed. During the 4 years of the experiment, we used some individuals in two (9 males, 14 females) or three (1 male) consecutive years. When this was the case, we used that individual in the same treatment group in the 2 years. In all these cases, however, these individuals paired up with different mates over the years. Male and female body condition (calculated by dividing body mass by (tarsus length)³, as in Griggio & Hoi, 2010), hatching date, brood size and age of nestling on the experimental day did not differ between the experimental groups (all $P > 0.05$).

Statistical Analysis

To examine whether parents compensate their parental behaviours in response to temporary removal of their partner, we investigated parental provisioning rate, latency and number of attacks in response to a model predator.

To evaluate provisioning behaviour when the mate was temporarily removed, we fitted linear mixed models (LMMs) with provisioning rate as response variable, phase (two categories: preremoval and postremoval), treatment (two categories: control versus mate-removed group), sex (two categories: male and female) and their three-way interaction as independent variables, while controlling for brood size, hatching date and offspring age. A significant three-way interaction in our experiment would indicate that feeding rates of male and female parents differed between phases depending on the treatment group. We then carried out post hoc tests on the LMMs to test differences between treatment groups and sexes. In these models, year was included as random effect. Because our experiment consisted in a within-individual comparison between phases and because we used some individuals over multiple years, our data set included two forms of repeated measures. For this reason, we first created an extra variable called 'Series ID' that took into account the pairwise values of each individual in the preremoval and the respective postremoval phase. At the same time, we also introduced a variable 'Bird ID' to consider the repeated measure of each individual over the years. We then included Series ID nested in Bird ID as random structure in the models to account for the repeated structure of the data set. Provisioning rate was log-transformed to improve normality of model residuals.

Second, we investigated how latency to approach the predator differed between the control and the mate-removed groups. Here,

we fitted a generalized linear mixed model (GLMMs) with latency as response variable and the same independent variables as the model described above. Bird ID and year were included as random effects. Because latency (s) to arrive in proximity to the nest was not normally distributed, but rather assumed a gamma distribution (i.e. asymmetrical distribution, where most of the data points occurred around the mean, with a long right tail given by long latencies), we modelled the variable latency as a gamma-distributed variable (family = gamma in the GLMMs) (Harrison et al., 2018; Lo & Andrews, 2015). Lastly, we investigated how the number of attacks directed towards the predator differed between parents in the control and the mate-removed groups. Because we did not observe any attack towards the predator in some nests, here we used zero-inflated Poisson models to model the number of attacks. We used number of attacks as the dependent variable and the same independent variables described for provisioning rate and latency. Bird ID and year were included as random effects. In these models, a significant interaction between treatment and sex would indicate that parents showed different parental responses when caring alone versus with their partner and that these differences differed between the sexes.

Lastly, we investigated whether provisioning and nest defence behaviours were correlated with each other at the individual level. Here we fitted three mixed models to explore the relationship between provisioning rate, latency and number of attacks and the relationship between latency and number of attacks. Also in these models, provisioning rate was log-transformed and latency was modelled as a gamma-distributed variable. The variable sex was also included in the models in interaction with the behavioural variables to explore sex differences in compensatory behaviours.

We performed all LMMs and GLMMs with the 'lmer' function in the 'lme4' package (Bates et al., 2015), while for the zero-inflated models, we used the 'glmmTMB' package (Brooks et al., 2017) in the R environment (R Core Team, 2017). To test significance of the main effects and interaction terms in the LMMs, we estimated degrees of freedom and *P* values of the *F* tests with the Kenward–Roger approximation implemented in the 'pbkrtest' package (Halekoh & Højsgaard, 2014). To assess differences between groups and sex, we carried out post hoc tests using the 'emmeans' function in the 'emmeans' package (Lenth, 2020). Significance was taken at $\alpha = 0.05$. Model assumptions were assessed via the 'performance' package (Lüdtke et al., 2021).

Ethical Note

Before conducting our experiment, we ensured that chicks belonging to the experimental nests were in good body condition to minimize adverse effects of the experiment on their growth and fledging. Mate removal was done by keeping the captured birds in a cotton bird bag, in the shade, for the shortest amount of time required for the experimental procedure (maximum 2.25 h). Upon release, all birds promptly left the bags, showing no evident signs of distress (e.g. immobility and/or unwillingness to escape). Short-term capture and restraining of wild animals in cotton bags (Cantarero et al., 2019) or shaded cages are unlikely to cause major distress or injury (Holt et al., 2009) or changes in body condition (Mortensen & Rosell, 2020). We noticed no desertion resulting from temporary removal of parents. We also did not observe strong year-to-year fluctuations in Spanish sparrow breeding density due to disappearance of experimental individuals, suggesting that handled birds and their offspring did not suffer any detectable reduction in welfare and survival. This study complies with the current laws on animal experimentation in Italy and the European Union. Permits were issued by the Istituto Superiore per la Protezione e la Ricerca Ambientale, Italy, licence no. 19828 to M.G.

RESULTS

For provisioning rate, we found a significant three-way interaction between the pre- and postremoval phases, treatment group and sex ($F_{7,147} = 20.81$, $P < 0.001$; Table 1). In particular, post hoc tests showed that parental provisioning rate differed between the pre- and the postremoval phase in the mate-removed groups (Fig. 1b, d, Table 2) but not in the control groups (Fig. 1a, c, Table 2). However, the magnitude of the compensatory responses to mate removal differed between sexes: 'widowed' males increased their provisioning rates by about 28%, while 'widowed' females compensated significantly more than males, by increasing their provisioning by about 68% (Fig. 1, post hoc tests in Table 2). Provisioning rate also increased slightly with hatching date (Table 1).

Latency to approach the predator differed between groups in the interaction with the sex of the parent (interaction term: $\chi^2_1 = 4.38$, $P < 0.036$; Table 1). Females showed the same latency to approach the predator regardless of whether they were in pairs or alone (Fig. 2a, Table 3). In contrast, males were slower to approach the predator than females, and when their partner was removed, they further increased their latency, on average, by 47% (Fig. 2a, Table 3). Latency at the nest also decreased as chick age increased (Table 1). Furthermore, the number of attacks toward the predator by the parents differed between control and mate-removed groups in the interaction with sex (interaction term: $\chi^2_1 = 33.51$, $P < 0.001$; Table 1). Females attacked the predator more intensely than males, but the number of their attacks did not vary when they were in pairs or alone (Fig. 2b, Table 3). Conversely, males attacked less intensely than females when in pairs and even less so (67% decrease) in the female-removed group (Fig. 2b, Table 3). These results indicate that the female did not compensate during

Table 1

Model estimates of the effects of treatment groups on overall provisioning rate, male and female provisioning rate

Variable	Estimate	SE	<i>t</i>	<i>P</i>
LMM for provisioning rate				
Intercept	0.77	0.12	6.60	<0.001
Phase (postremoval)	-0.04	0.02	-2.14	0.035
Treatment (removal)	0.01	0.02	0.31	0.759
Sex (male)	-0.03	0.02	-1.48	0.142
Brood size	0.01	0.01	1.12	0.266
Offspring age	-0.01	0.01	-1.02	0.310
Hatching date	0.01	0.01	3.04	0.003
Phase (postremoval)*treatment (removal)	0.23	0.03	7.56	<0.001
Phase (postremoval)*sex (male)	0.02	0.02	0.85	0.398
Treatment (removal)*sex (male)	0.03	0.03	0.96	0.335
Phase (postremoval)*treatment (removal)*sex (male)	-0.15	0.04	-3.73	<0.001
GLMM for latency				
Intercept	-2019.95	6461.73	-0.31	0.755
Treatment (removal)	8.62	6.46	1.33	0.182
Sex (male)	27.73	8.64	3.21	0.001
Brood size	-0.53	3.20	-0.17	0.867
Offspring age	-12.56	4.41	-2.84	0.004
Hatching date	1.40	0.85	1.64	0.101
Treatment (removal)*sex (male)	35.29	16.85	2.09	0.036
GLMM for number of attacks				
Intercept	2.12	0.89	2.37	0.018
Treatment (removal)	0.03	0.10	0.30	0.763
Sex (male)	-0.39	0.11	-3.55	<0.001
Brood size	-0.00	0.04	-0.13	0.897
Offspring age	-0.02	0.07	-0.25	0.806
Hatching date	0.01	0.01	1.16	0.247
Treatment (removal)*sex (male)	-1.15	0.20	-5.79	<0.001

P values < 0.05 are indicated in bold. Control group and female are, respectively, treatment group and sex of reference.

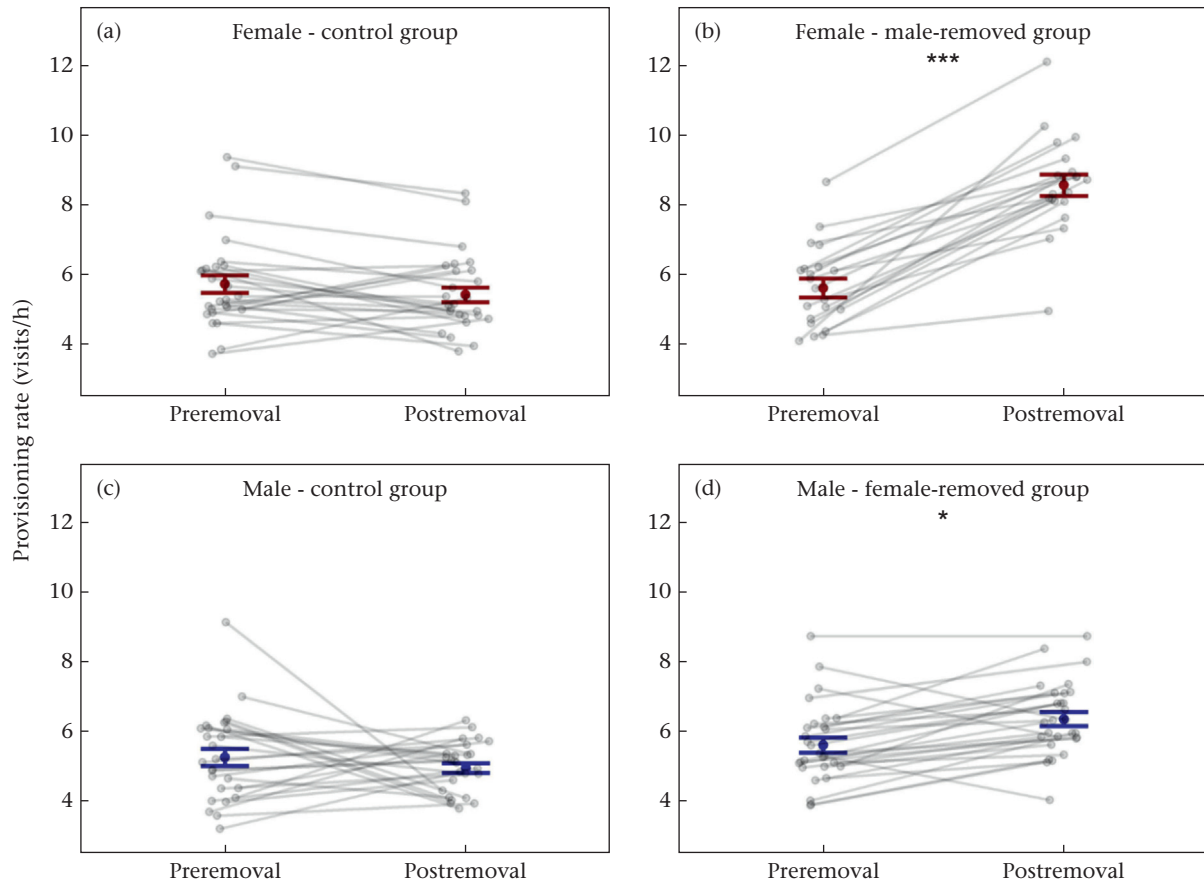


Figure 1. Within-individual changes in provisioning rate between the preremoval and postremoval phase for females and males in the control (a, c) and mate-removed groups (b, d). Asterisks indicate significant within-individual changes.

predator defence after male removal and that males decreased their investment in the brood.

Among the three behaviours we measured (provisioning rate, latency, attack intensity towards the predator) in response to mate removal, only some were correlated with each other at the individual level. Specifically, we did not find a significant correlation between provisioning rate and latency (Fig. 3a, Table 4), nor did we find a significant relationship between provisioning rate and

number of attacks towards the predator (Fig. 3b, Table 4). In contrast, latency to approach the predator was negatively correlated with number of attacks, but only in males, indicating that males were slower to approach the predator and performed fewer attacks than females (Fig. 3c, Table 4).

DISCUSSION

We used a within-individual approach to experimentally investigate whether Spanish sparrow parents modify their parental investment (offspring provisioning and predator defence) after short-term mate removal. We found indications that parents differed in their compensatory responses in relation to parental task and sex: both sexes partially compensated for offspring provisioning, but females compensated by a larger degree than males. In contrast, for predator defence, males decreased defence behaviour by increasing latency and reducing the number of attacks, while females did not change their behaviour when caring alone.

To our knowledge, this is the first study in which parental compensatory responses have been investigated on two parental tasks simultaneously, offspring provisioning and nest defence behaviour. According to the prediction of the theoretical models (Johnstone & Hinde, 2006; McNamara et al., 1999), we found that parents partially compensated their provisioning visits when caring alone for the offspring. This result is in line with several previous studies in birds (Harrison et al., 2009), as well as our finding of a sex difference in the magnitude of compensation, with females compensating more than males (Griggio & Pilastro, 2007; Sanz et al., 2000; Smiseth et al., 2005). The observed increase in

Table 2

Tukey post hoc tests on parental provisioning rate across phases and across groups in the postremoval phase

Variable	Estimate	SE	<i>t</i>	<i>P</i>
Tukey post hoc tests on provisioning rate across phases				
Female preremoval control – female postremoval control	0.04	0.02	2.14	0.147
Female preremoval treatment – female postremoval treatment	–0.18	0.02	–8.24	<0.001
Male preremoval control – male postremoval control	0.02	0.02	0.93	0.786
Male preremoval treatment – male postremoval treatment	–0.05	0.02	–2.87	0.025
Tukey post hoc tests on provisioning rate across groups				
Female control – male control	0.01	0.02	0.40	0.979
Female control – female alone	–0.24	0.02	–9.77	<0.001
Male control – male alone	–0.11	0.02	–5.02	<0.001
Female alone – male alone	0.13	0.02	5.61	<0.001

P values < 0.05 are indicated in bold.

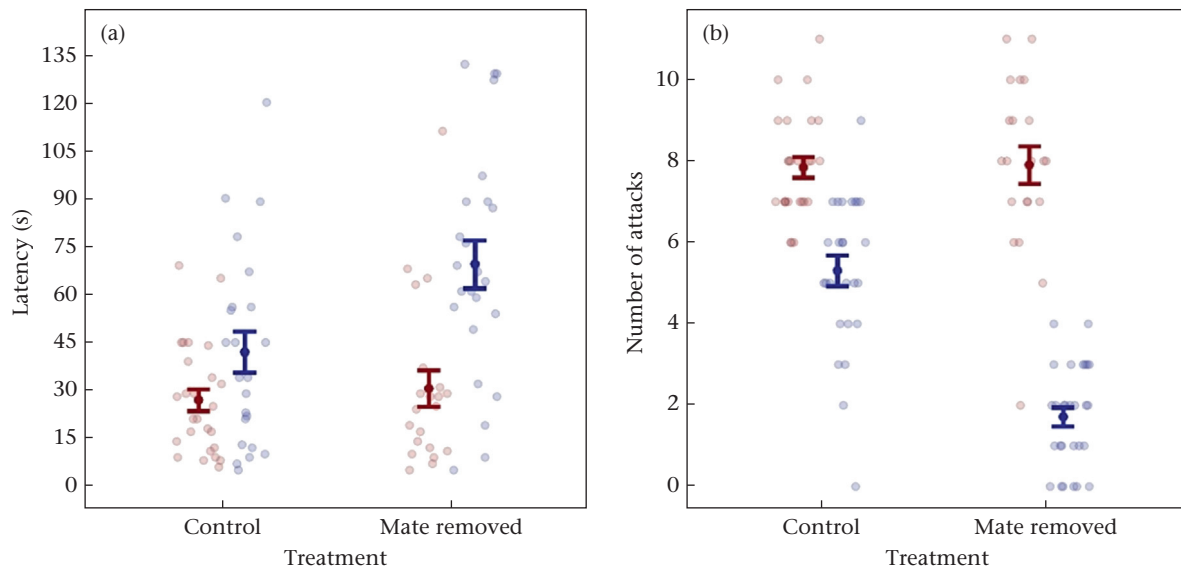


Figure 2. (a) Latency to approach a predator and (b) number of attacks towards the predator during the postremoval phase in the control (both parents are present) and the mate-removed treatment groups. Mean \pm SE is shown. Red symbols: females; blue symbols: males.

provisioning rate of the focal parent in the absence of its mate is expected given that there is general agreement that parents do not generally provision at their maximum rate (Nur, 1984). In fact, brood size manipulation experiments have consistently found that parents can increase provisioning rate on short timescales when the number of offspring is experimentally increased (Baldan et al., 2019; Gow & Wiebe, 2014; Hinde & Kilner, 2007; Mariette & Griffith, 2015). Therefore, provisioning parents may be able to increase their working rate and compensate for the lack of the partner, at least in the short term.

The occurrence of partial compensatory responses in provisioning rate in our study can have multiple concomitant explanations. First, mate removal manipulations can influence cost functions associated with provisioning/investing alone (McAuliffe et al., 2015). Group provisioning can enhance food discovery and foraging success (Alexander, 1974; Krause & Ruxton, 2002; Snijders et al., 2021; Tóth et al., 2017) and reduce predation risk due to dilution and confusion effects (Carranza et al., 2008; Foster & Treherne, 1981; Turner & Pitcher, 1986), and recent evidence shows that songbird parents forage together and coordinate their provisioning trips to the offspring (Baldan & van Loon, 2022). Therefore, when provisioning alone, the widowed parents in our experiment could have experienced higher costs of provisioning by lacking these two positive effects of group provisioning. To better understand whether the partial compensation we observed was driven by the benefit and cost functions associated with provisioning behaviour, concomitant

experiments of mate removal and weight loading on the focal parents, which increases the cost of provisioning, could be valuable approaches to determine the extent to which compensation is expected. For instance, by increasing the cost of provisioning by weight loading, we would expect parents to decrease the optimal compensatory response. Other explanations for partial compensation could be (1) that a lack of investment by the removed partner could also be perceived by the focal parents as a reduced brood need or value (Johnstone & Hinde, 2006) or (2) the response of the (temporarily) deserted parent may require time, because a response that is too rapid may easily be exploited by the partner to further decrease its provisioning rate (Lessells & McNamara, 2012). A delayed response to the partner's reduction of provisioning rate may also be expected if the response is mediated by nestlings' signals of need, which also may take time to be fully expressed. Furthermore, even in this case, a delayed response of the parent to nestling signalling may be favoured in the context of parent–offspring conflict. Therefore, individual decisions over how much to compensate for partner removal may be driven by multiple concomitant factors, such as the benefits and costs of additional investment, the temporal pattern of negotiation (Iserbyt et al., 2017; Sowersby et al., 2017) and the altered perception of brood state (Johnstone & Hinde, 2006).

Our experimental presentation of a predator at the nest site resulted in no change in nest defence behaviour by the females but a lower parental investment in terms of longer latencies and fewer attacks by males when caring alone rather than in pair. These results contrast with our initial predictions, in which we expected a higher compensatory behaviour by the remaining parent due to the expected linear benefits of each single attack towards the predator. One possibility for a lack of compensation for 'widowed' parents is that nest defence and aggression towards a predator is associated with a high mortality risk for the parents (Montgomerie & Weatherhead, 1988; Regelman & Curio, 1986). When attacking the predator alone, the parent can suffer a higher per capita rate of injury compared to defending the nest as a pair due to dilution and confusion effects (Foster & Treherne, 1981; Turner & Pitcher, 1986). This would lead to increased potential costs, ultimately resulting in lower nest defence behaviour for widowed parents, as we observed in this study, although for males only. Our results are also in line with a similar study conducted in great reed warblers, *A. arundinaceus*, exposed to simulated predator intrusions (Trnka &

Table 3
Tukey post hoc tests on latency and number of attacks in the postremoval phase

Variable	Estimate	SE	<i>t</i>	<i>P</i>
Tukey post hoc tests on latency				
Female control – female alone	–8.63	6.46	–1.33	0.540
Male control – male alone	–43.91	15.70	–2.80	0.026
Female control – male control	–27.74	8.65	–3.21	0.007
Female alone – male alone	–63.02	14.46	–4.36	<0.001
Tukey post hoc tests on number of attacks				
Female control – female alone	–0.03	0.10	–0.30	0.99
Male control – male alone	1.11	0.17	6.59	<0.001
Female control – male control	0.39	0.11	3.55	0.003
Female alone – male alone	1.53	0.16	9.34	<0.001

P values < 0.05 are indicated in bold.

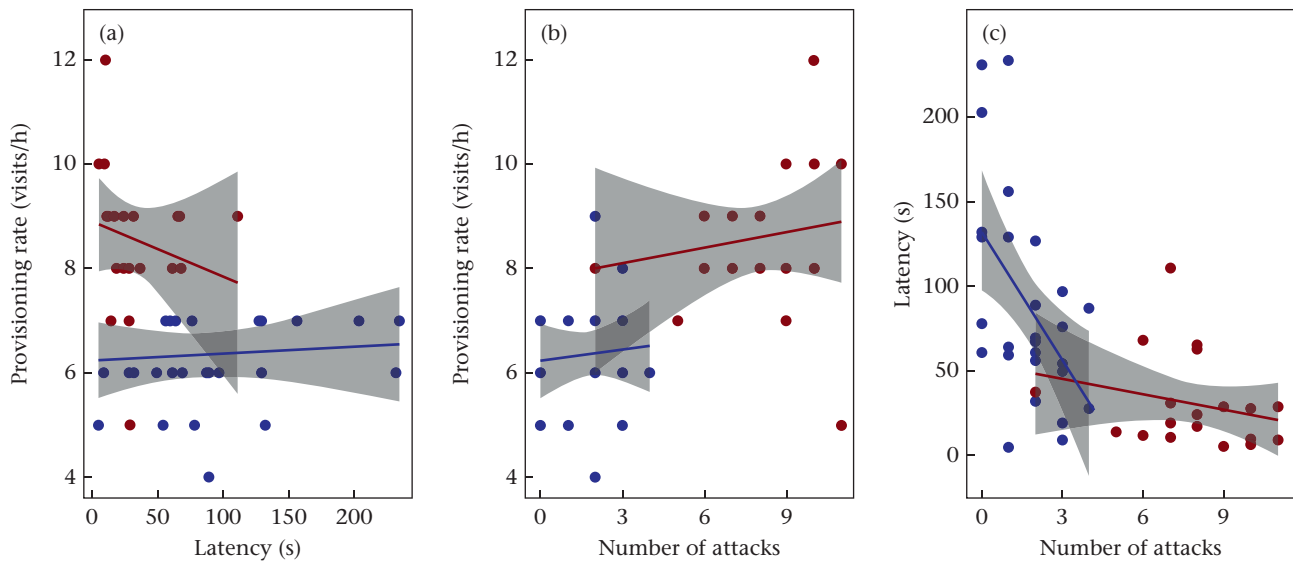


Figure 3. Relationship between (a) provisioning rate and latency to approach the predator, (b) provisioning rate and number of attacks towards the predator and (c) latency and number of attacks towards the predator during the postremoval phase in the mate-removed treatment group. Red symbols: females; blue symbols: males.

Grim, 2012). Here the authors found that females did not vary their defence level according to their partner's presence and that males defended their nests less when they were alone. So why would female and male parents respond differently to mate removal in terms of nest defence? One explanation could be that a female's parental behaviour is less affected by her mate's activity and more affected by offspring need (Hinde & Kilner, 2007). In our study, similarly to Trnka and Grim (2012), females were also faster to approach the model predator compared to males, so it could be that a male's decisions on intervention and predator defence depend more on his partner's behaviour. Another possibility is that males might have more opportunities than females to breed again later on, as males in this species have been observed performing mating displays during the second half of the chick provisioning period (Metzmacher, 1990). Thus, a potential asymmetry in re-nesting opportunity and future survival (Griffith et al., 1999; Murphy, 1978; Tavecchia et al., 2002) between the sexes could determine why uniparental females invest more than uniparental males in nest defence and exhibit more parental investment to the current brood.

Table 4

Model estimates for the correlations between provisioning rate, latency to approach a predator and number of attacks to the predator

Variable	Estimate	SE	<i>t</i>	<i>P</i>
Relationship between provisioning rate and latency				
Intercept	0.95	0.03	33.76	<0.001
Latency	0.00	0.00	-1.83	0.093
Sex (male)	-0.16	0.03	-4.94	<0.001
Latency * sex (male)	0.00	0.00	1.90	0.073
Relationship between provisioning rate and number of attacks				
Intercept	0.90	0.06	14.70	<0.001
Number of attacks	0.00	0.01	0.47	0.469
Sex (male)	-0.10	0.06	-1.63	0.111
Number of attacks * sex (male)	0.00	0.01	-0.03	0.974
Relationship between latency and number of attacks				
Intercept	53.88	24.03	2.24	0.025
Number of attacks	-3.29	2.80	-1.17	0.240
Sex (male)	66.31	30.74	2.16	0.031
Number of attacks * sex (male)	-17.35	7.57	-2.29	0.022

P values < 0.05 are indicated in bold.

We also found that, when alone, males were slower to detect predators at the nest site (higher latency). As latency is considered a proxy for defence and presence at the nest site (Matessi et al., 2009; Trnka & Grim, 2012), longer latencies to detect predators could occur when parents forage farther from the nest. If so, 'widowed' males could actively reduce their presence at the nest and increase their foraging area to promote the discovery of new food patches (Komdeur & Kats, 1999). In this experiment, we had no information about the movements and foraging patterns of our Spanish sparrow parents. The use of radiotracking (Baldan & van Loon, 2022; Bircher et al., 2020) or GPS devices (Cagnacci et al., 2010; Hallworth & Marra, 2015) will be helpful to further investigate parental responses to mate removal and sex differences.

Our experimental set-up also allowed us to quantify each individual's parental responses to mate removal for two distinctive parental tasks. This allowed us to assess whether Spanish sparrow parents have different compensatory strategies and/or specialize in specific parental tasks (Barta et al., 2014; McNamara & Wolf, 2015). We found that, in general, males and females equally contributed to offspring feeding in unmanipulated biparental conditions, but that females contributed more than males to nest defence. However, we did not find any indication that individuals, within each sex, allocated their compensatory responses primarily to one task (e.g. devoted more investment to offspring feeding than to predator defence), with the exception that males that had shorter latencies to attack the predator also had higher attack rates. Therefore, Spanish sparrows do not appear to have strong individual variation in caring or negotiation rules. Further experimental manipulation on partner contributions on different parental tasks could help to better understand the role of individual variation in promoting sex roles within families (Long & Weissing, 2020).

Our study demonstrates that parental compensatory strategies to experimental reduction of partner contribution vary between parental tasks, and that such differences may arise due to different cost and benefit functions of extra investment and/or the level of risk imposed on the parent. In particular, the benefit and cost functions of parental behaviours may differ when parents are caring alone or in pairs. We strongly encourage further negotiation models and empirical studies that span different parental tasks to investigate how individuals should 'optimally' respond to variation in parental care strategies by their partners.

Author Contributions

M.G. and A.A.P. conceived the study. M.G. collected the data. M.S. and D.B. analysed the data and wrote the paper. M.S., A.A.P. and D.B. revised, edited and approved the manuscript before submission.

Data Availability

The raw data for this study are available from Zenodo (<https://doi.org/10.5281/zenodo.7702758>).

Declaration of Interest

We declare we have no competing interests.

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