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Pair coordination is related to later brood desertion in a provisioning songbird

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Raising a family is not free of conflict for parents, as each parent benefits when its partner provides more care for the offspring. Resolving this conflict requires cooperation between the parents. One way to achieve such cooperation might be to coordinate parental provisioning by synchronizing (i.e. returning to the nest at the same time) or alternating (i.e. taking turns) offspring provisioning at the nest. Empirical studies in birds indicate that pair coordination of the nest visits is common; however, it is unknown whether this behaviour is directly related to different outcomes of sexual conflict, such as brood desertion. We used the rock sparrow, *Petronia petronia*, a species with high levels of sexual conflict, to explore whether alternation and synchrony of the nest visits were related to later brood desertion. Pairs with no desertion alternated and synchronized their nest visits more than pairs in which one sex deserted. This difference in coordination was not simply a by-product of differences in provisioning by the parents. Synchrony of the visits also increased with offspring age in the pairs with no desertion. We provide evidence, for the first time to our knowledge, that the degree of parental coordination is strongly associated with the ultimate consequence of sexual conflict, brood desertion, supporting the idea that coordination in parental behaviour might promote conflict resolution.

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As parental care is costly, there exists significant sexual conflict between parents over the amount and duration of care that each parent devotes to the offspring (Trivers, 1972). In species in which males and females care for the young together, one possible outcome of this conflict is to desert the offspring: one parent stops caring before the young become independent (Székely, Webb, Houston, & McNamara, 1996). By deserting, a parent may increase its own survival by reducing care for the deserted brood (Barta, Houston, McNamara, & Székely, 2002; Olsson, 1997; Székely, Cuthill, & Kis, 1999) or may increase its reproductive success by remating in the same breeding season (Griggio, Matessi, & Pilastro, 2005; Pilastro, Biddau, Marin, & Mingozzi, 2001). On the other hand, by helping its mate raise the young, a parent may increase its fitness via the current offspring (reviewed by Székely et al., 1996). Therefore, each parent faces an important decision while provisioning the young: to collaborate with its mate or to desert the brood.

Several studies have investigated different ecological and biological factors that can affect the individual decision to desert the brood, such as brood size (Beissinger, 1990; Winkler, 1991), perceived paternity (Westneat & Sherman, 1993), offspring quality (Erikstad et al., 1997), mate attractiveness (Johnsen, Lifjeld, & Rohde, 1997), number of potentially available partners (Pilastro et al., 2001) or timing of reproduction (Griggio, 2015). However, a crucial yet overlooked mechanism that may influence the decision to care for or to desert the brood could be pair coordination of parental provisioning (Johnstone et al., 2014; Mariette & Griffith, 2012; Raihani, Nelson-Flower, Moyes, Browning, & Ridley, 2010; Savage, Browning, Manica, Russell, & Johnstone, 2017). Pair coordination, specifically synchrony and alternation of the nest visits, represents patterns of nest provisioning, which result from active behavioural interactions between the parents (Johnstone et al., 2014; Mariette & Griffith, 2015; Raihani et al., 2010; Savage et al., 2017). In particular, synchrony of the nest visits occurs when parents visit the nest together to feed the offspring because they forage in the same patch (Mariette & Griffith, 2015) and actively wait for the partner to return together to the nest (Raihani et al., 2010). Alternation of the nest visits represents a provisioning pattern in which a visit by one parent is followed by a visit of its partner because parents take turns of visits over time (Johnstone et al.,

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2014; Savage et al., 2017). These patterns of coordinated visits have been found in several avian species (Bebbington & Hatchwell, 2016; Iserbyt, Fresneau, Kortenhoff, Eens, & Muller, 2017; Koenig & Walters, 2016; Leniowski & Węgrzyn, 2018; Mariette & Griffith, 2012; Raihani et al., 2010; Shen, Chen, Vehrencamp, & Yuan, 2010) with growing evidence that such coordination increases parents' and offspring's fitness via reduced risk of predation at the nest (Bebbington & Hatchwell, 2016; Leniowski & Węgrzyn, 2018; Raihani et al., 2010) and more equal food partitioning to the offspring (Shen et al., 2010). More importantly, coordination of provisioning has been suggested to reduce conflict over shared investment between the parents (Johnstone et al., 2014) because by synchronizing or alternating their visits, parents can maintain equal share of the care and monitor the investment level of the partner. In this regard, there is evidence in zebra finches, *Taeniopygia guttata*, that parents increase cooperation and coordination of the provisioning when parents were experimentally induced to work harder for the offspring (Mariette & Griffith, 2015). However, our understanding of pair coordination as a mechanism ameliorating conflict between the parents is based so far on species with a low level of sexual conflict (Remeš, Freckleton, Tökölyi, Liker, & Székely, 2015), and there is currently no direct investigation of how pair coordination is related to different outcomes of sexual conflict, such as brood desertion.

The rock sparrow, *Petronia petronia*, is an ideal system to explore how pair coordination can affect the decision to desert or collaborate with the mate. This species has a highly variable system of biparental care in which some males provide care together with females during the first week after hatching and then gradually decrease their provisioning as nestlings age. This can occur to the extent that, some days before nestlings fledge (day 18 of chick rearing), approximately 25% of males desert the brood (see Griggio et al., 2005). More rarely, brood desertion occurs by females (approximately 10% of females) and males then care exclusively for the nestlings (Griggio, 2015; Griggio et al., 2005).

In this study, we used parental provisioning data during chick feeding and investigated whether pair coordination, in terms of alternation and synchrony of the nest visits during offspring provisioning, is related to later brood desertion. In particular, we expected that, if pair coordination can reduce the sexual conflict between parents, pairs with more alternated and synchronized visits would be less likely to experience brood desertion than pairs with low levels of coordination.

METHODS

Study Species

The rock sparrow is a short-lived species (average life span of ca. 1.5 years, M. Griggio, personal observation) with a relatively high extrapair paternity rate (32.0% of the chicks are not sired by the social father and 54.8% of the broods contain at least one extrapair young; Pilastro et al., 2001). Rock sparrows breed from May to the end of July, usually once with a low percentage of second clutches (below 20%, M. Griggio, personal observation). The brood size in this population is ca. five nestlings (García-Navas, Valera, & Griggio, 2015). Rock sparrows usually breed with a different partner over different breeding attempts (M. Griggio, personal observation).

Data Collection

We studied a Sardinian population of rock sparrows in Barbagia (40°23'30"N, 9°12'12"E, 700 m above sea level) between 2007 and 2014. A mean of 36 nestboxes were set up from 2007 (for more details see García-Navas et al., 2015; Griggio, 2015). The population

included approximately 20 breeding pairs each year. Nestboxes were also designed to work as traps, so adults could be individually colour ringed and measured. Each year, we checked the nestboxes every second or third day from the start of the breeding season (May) until the last chicks fledged (July). In this study, we used 54 pairs (22 pairs without desertion, 17 with male desertion, 15 with female desertion) of first broods. These nests did not include ones involved in manipulation experiments (García-Navas et al., 2015), and we only included the first breeding attempts of all individuals to avoid pseudoreplication. Brood size did not differ between groups (generalized linear model, GLM, on number of offspring: $\chi^2_2 = 0.10$, $N = 54$, $P = 0.950$; no desertion: 4.6 ± 0.16 (brood size mean \pm SE); male desertion: 4.88 ± 0.22 ; female desertion: 4.86 ± 0.23). Each nest was observed for 1 h in the morning (between 0600 and 1030 hours) on 1 day during chick rearing (7.30 ± 0.77 , mean \pm SD of offspring age during the behavioural observation) with 20×60 spotting scopes while sitting in the open, approximately 30–50 m from the nest. We observed parental provisioning behaviour around day 7 of chick age because in this period (1) females usually stop brooding at the nest because chick can thermoregulate and (2) both parents devote most of their time to provisioning (Griggio & Pilastro, 2007). For each observation period, we scored the time of each parental visits (time of entry in the nestbox to the nearest 1 s) and the identity of the parent. Brood desertion was confirmed when one parent was no longer observed at the nest and was seen at a second nest (for more details see Pilastro et al., 2001). The remaining parent was observed until the brood successfully fledged.

From the sequence of nest visits, we calculated their alternation and synchrony. We defined alternated visits as visits of one individual that followed a visit of its mate. For the calculation of alternation from a sequence of nest visits (e.g. MMFMFMFFM), visits can occur at any time, and by either parent, after the previous one. We expected different amounts of alternation to arise by chance in a sequence of visits depending on the proportion of visits by the two parents. In situations in which, for instance, one parent makes either all or none of the visits in a sequence, no alternated visits can occur. Conversely, when parents feed the offspring at similar rates, the proportion of alternated visits we expected by chance increases. To account for this effect, we used an alternation score to measure the deviation of the observed amount of alternation from that expected given the relative contributions (provisioning rates) of the two parents as follows:

$$\text{Alternation score} = \log \left(\frac{\text{Observed no. of alternated visits}}{\text{Observed no. of nonalternated visits}} \right) - \log \left(\frac{\text{Expected no. of alternated visits}}{\text{Expected no. of nonalternated visits}} \right)$$

See Baldan, Curk, Hinde, & Lessells (2019) for a detailed explanation of the calculation of the alternation score. An alternation score of zero represents the amount of alternation expected by chance, a value of less than 0 means that the observed alternation of the visits is lower than expected by chance, and a value of greater than 0 means that the observed alternation of the visits is greater than expected by chance. We also calculated the proportion of synchronized visits as the number of synchronized visits over the total number of visits. Synchronized visits were defined as one visit by each parent occurring within 1 min of each other. As in a previous study (Bebbington & Hatchwell, 2016), we used a 1 min window to calculate synchrony to minimize the risk that synchronized visits could occur by chance. Males and females visited the nest on average 5.1 and 6.8 times/h, respectively. If parents were visiting the nest independently from each other, we would

expect that less than 1% [(5.1 male visit rate/60 s) × (6.8 female visit rate/60 s)] of parental visits would occur within 1 min of each other by chance.

Statistical Analysis

To explore whether pair coordination differed between deserting and nondeserting pairs, we first explored parental provisioning rates. We fitted linear models (LMs) with overall provisioning rate (male and female visits combined) and individual provisioning rate (male and female visits separately) as response variables, 'group' (no desertion, male desertion, female desertion) and 'year' as factors and 'offspring age' (the offspring age during the behavioural observation) as a covariate. For the individual provisioning rates, we also tested the interaction between 'sex' and 'group'. We also investigated whether the proportion of visits by the parents differed between the groups. We fitted GLMs with proportion of visits by the male as the response variable, 'group' and 'year' as factors and 'offspring age' as a covariate.

We investigated whether alternation differed between deserting and nondeserting pairs. We fitted LMs with alternation score as the response variable, and included the same covariates used in the previous models. We explored whether synchrony varied between groups by fitting GLMs with proportion of synchronized visits as the response variable, 'group' (no desertion, male desertion, female desertion) and 'year' as factors and 'offspring age' as a covariate. We also included 'total number of visits' and 'proportion of male visits' in this analysis, as we expected (1) the number of synchronized visits to decrease as the difference in proportion of feeds by the two parents increased and (2) synchrony to increase at higher feeding rates, as it increases the chance that two visits can occur within 1 min of each other. In this analysis, we specifically investigated whether the difference in synchrony between groups could arise even if the deserting parent might have already reduced its contribution in terms of provisioning (see [Results](#)).

Lastly, we investigated whether fledgling success differed between nests in relation to parental desertion. We fitted GLMs with number of fledglings and fledgling success (proportion of fledged chicks over original number of chicks) as response variables and 'group' (no desertion, male desertion, female desertion) and 'year' as factors.

All the statistical analyses were performed in the R environment version 3.2.3 ([R Development Core Team, 2017](#)). As brood size did

not differ by group, feeding rate did not correlate with brood size and brood size was not significant in all models, we excluded brood size from the final models. In all models, we first tested whether interaction terms were significant, for example sex and group, and removed the interaction term when it was nonsignificant. All tests of fixed effects are two tailed and with a significance level set to $\alpha = 0.05$.

Ethical Note

This study complies with the current laws on animal experimentation in Italy and the European Union. The long-term nature of the study allowed us to confirm that handled birds and their offspring did not suffer any detectable reduction in welfare and survival. Permits were issued by the Istituto Superiore per la Protezione e la Ricerca Ambientale, Italy, licence no. 19828.

RESULTS

Provisioning rates at the nest differed slightly between groups ([Table 1](#), [Fig. 1a](#)): broods with no desertion received more visits than broods in which one parent later deserted the nest. This occurred because parents changed their feeding rates between groups in interaction with sex ($F_2 = 7.47$, $P < 0.001$; [Fig. 1b](#)). In particular, males had lower provisioning rates when they later deserted the brood ([Table 1](#)), whereas we found a marginally nonsignificant trend that females also lowered their provisioning rates in the female desertion group ([Table 1](#)). These changes in parental provisioning rate also resulted in different proportions of visits by the parents between the groups ([Table 2](#), [Fig. 1c](#)).

Alternation score was significantly higher in nondeserted pairs compared to pairs with male or female desertion ([Table 3](#), [Fig. 2a](#)). In addition, the proportion of synchronized visits changed significantly with the interaction of offspring age and group ($\chi^2_2 = 11.53$, $P = 0.003$), while controlling for provisioning rate and relative proportion of feeds by the two parents ([Table 3](#)). Specifically, synchronized visits increased with offspring age in pairs with no desertion and decreased with offspring age when females deserted ([Table 3](#), [Fig. 2b](#)).

Reproductive success did not differ between the three desertion groups (number of fledglings: $\chi^2_2 = 0.276$, $P = 0.871$; fledgling success: $\chi^2_2 = 4.304$, $P = 0.116$).

Table 1
Model estimates of the effects of groups on overall provisioning rate, male and female provisioning rate

Variable	Estimate	SE	t	P
LM for overall provisioning rate ($R^2=0.05$)				
Intercept	16.61	203.19	-0.082	0.93
Year	-0.00	0.10	-0.021	0.98
Offspring age	0.02	0.24	-0.098	0.92
Male desertion group compared to control	-0.80	0.38	-2.086	0.042
Female desertion group compared to control	-0.91	0.40	-2.277	0.027
LM for male provisioning rate ($R^2=0.11$)				
Intercept	33.88	243.56	0.139	0.89
Year	-0.01	0.12	-0.125	0.90
Offspring age	0.27	0.28	0.983	0.33
Male desertion group compared to control	-1.27	0.46	-2.754	0.008
Female desertion group compared to control	0.13	0.48	0.267	0.790
LM for female provisioning rate ($R^2=0.08$)				
Intercept	-17.27	270.25	-0.064	0.95
Year	0.01	0.13	0.097	0.92
Offspring age	-0.26	0.31	-0.812	0.42
Male desertion group compared to control	0.47	0.51	0.914	0.365
Female desertion group compared to control	-1.03	0.52	-1.953	0.056

All groups are compared with the control, which is no desertion. P values < 0.05 are indicated in bold.

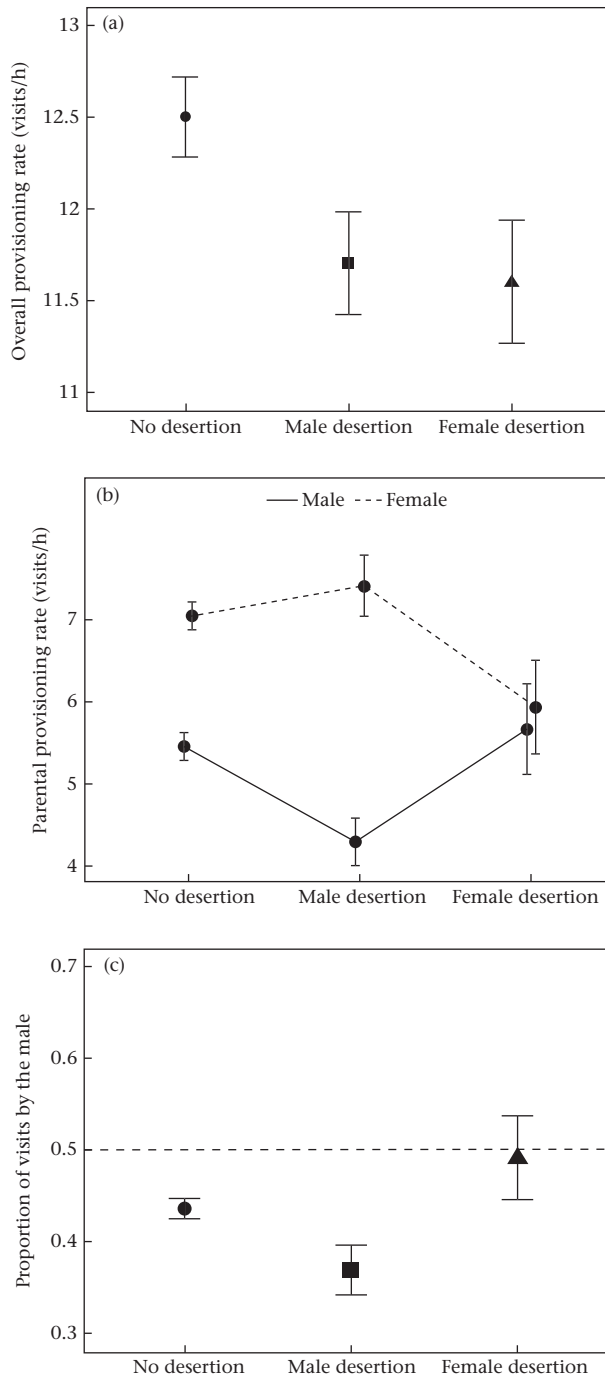


Figure 1. (a) Overall provisioning rate (male and female visits combined), (b) provisioning rates of male and female parents and (c) proportion of visits by the male for broods with no, male or female desertion. Dashed line in (c) represents equal proportion of visits by the two parents. Bars show means and SE of the mean.

Table 2
Model estimates of the effects of groups on proportion of visits by the male

Variable	Estimate	SE	χ^2	df	P
GLM for proportion of male visits ($R^2=0.10$)					
Year			0.015	1	0.901
Offspring age			0.684	1	0.408
Group (no desertion)	11.49	100.34	6.163	2	0.046
Group (male desertion)	11.16	100.34			
Group (female desertion)	11.68	100.38			

P values < 0.05 are indicated in bold.

Discussion

Using a system with a high level of sexual conflict in which both parents can desert the brood, we explored a possible mechanism by which parents can resolve sexual conflict. More coordinated parents, that is, those that had highly synchronized and alternated visits, were those that did not desert their nest. Furthermore, parental synchrony of the nest visits increased with offspring age only for pairs with no desertion.

Our results represent a snapshot of parental feeding during chick rearing and showed a relationship between the level of pair coordination and the likelihood that one parent later deserts the nest. One explanation for this pattern is that, when the data were collected, the deserting parents had already decreased their contribution to the offspring, such that the lower coordination in deserting pairs was a by-product of imminent desertion. Indeed, parents in this species that desert the nest gradually decrease their provisioning throughout the chick-rearing period (Griggio et al., 2005). However, our results show that differences in provisioning rates and relative proportion of feeds by the parents do not entirely explain the difference in coordination between the groups, indicating that pairs differ in their level of coordination regardless of the potential effect of a parent reducing its workload. This suggests that early levels of pair coordination may predict the likelihood of a parent deserting the nest: pairs with high levels of coordination may be less prone to divorce than pairs with low coordination. We only had one observation per nest, so we could not test whether pairs that show a higher initial level of coordination are less likely to desert the brood. Multiple observations per nest during the rearing period are therefore necessary to better investigate the causal relationship between pair coordination and brood desertion.

Our results support a recent theoretical model suggesting that pair coordination, such as alternation of the nest visits, can reduce conflict between the parents (Johnstone et al., 2014), as we found evidence that the degree of parental coordination is correlated with an extreme outcome of sexual conflict: brood desertion. Why should parental coordination promote investment in the current offspring over brood desertion? One explanation is that parental coordination allows parents to work at their maximum rate because parental investment can no longer be exploited by the partner (Johnstone et al., 2014). In addition, empirical studies in bird species show that pair coordination is beneficial in terms of increased brood survival (Raihani et al., 2010), offspring mass (Mariette & Griffith, 2015) and reduced predation risk (Leniowski & Węgrzyn, 2018). Given these potential benefits of coordination, it may be more beneficial for parents to invest in the current offspring rather than deserting the nest. However, in our data set we did not find any differences in fledging success between deserting and non-deserting nests, so the direct fitness consequences of desertion for parents are not completely clear. Investigating offspring recruitment and/or parental survival may provide more insight on the costs and benefits of brood desertion. Another nonmutually exclusive explanation of the observed lower desertion in coordinated pairs might be mate guarding during chick provisioning. By coordinating the provisioning activity, parents may be able to monitor each other, lowering the chance that the partner engages in extrapair activities (but see Griggio & Venuto, 2007). If searching for an extra mate occurs with more time lost for an individual or the chances of finding an extrapair mate are reduced when the current partner monitors its mate, then it is beneficial to stay with the current brood.

Given the ample benefits of coordination, why do some pairs show low levels of coordination that results in one parent deserting the brood? One possibility is that pair coordination might be related to parental quality, behavioural compatibility (Ihle,

Table 3
Model estimates of the effects of groups on alternation score and synchrony

Variable	Estimate	SE	<i>t</i>	<i>P</i>
LM for alternation score ($R^2=0.52$)				
Intercept	-2.86	110.33	-0.026	0.98
Year	0.00	0.05	0.042	0.97
Offspring age	-0.07	0.13	-0.549	0.58
Male desertion group compared to control	-1.30	0.21	-6.241	<0.001
Female desertion group compared to control	-1.38	0.22	-6.640	<0.001
GLM for proportion of synchronized visits ($R^2=0.50$)				
Intercept	112.09	125.15	0.896	0.37
Total number of visits	0.25	0.11	2.345	0.02
Proportion of male visits	2.10	1.24	1.686	0.09
Offspring age	0.71	0.22	3.271	0.001
Year	-0.06	0.06	-0.975	0.33
Male desertion group compared to control	-1.42	3.38	-0.418	0.68
Female desertion group compared to control	6.29	2.91	2.381	0.02
Offspring age*Male desertion group	-0.10	0.43	-0.229	0.82
Offspring age*Female desertion group	-1.15	0.41	-2.828	0.005

All groups are compared with the control, which is no desertion. *P* values < 0.05 are indicated in bold.

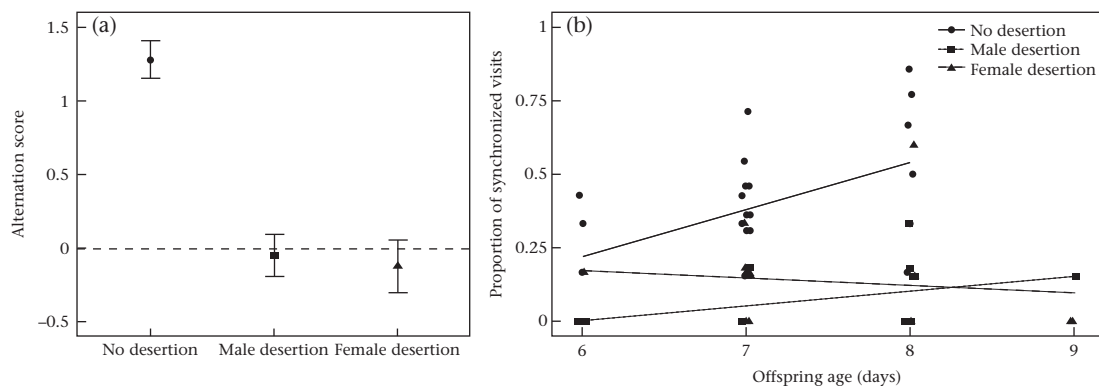


Figure 2. (a) Alternation score in pairs that had no, male or female desertion. An alternation score of zero (dashed line) represents the amount of alternation expected by chance. Bars show means and SE of the mean. (b) Synchrony of the nest visits in relation to offspring age in pairs with no, male or female desertion.

Kempnaers, & Forstmeier, 2015; Spoon, Millam, & Owings, 2007) or partner familiarity/experience (Griggio & Hoi, 2011; Nol & James, 1987). In rock sparrows, parents almost never breed together over multiple breeding attempts, so it is unlikely that pair familiarity plays an important role in this species. On the other hand, parental quality or behavioural compatibility within pairs might be key factors driving provisioning coordination. In this scenario, better or more compatible parents might be able to achieve higher coordination, making it more beneficial for them to keep investing in the offspring and vice versa. To support this idea, we found that synchrony of the nest visits increased with offspring age only in pairs with no desertion, whereas synchrony decreased slightly in pairs with female desertion. This finding might indicate the intriguing idea that pair coordination is flexible, and that some pairs increase their level of coordination, ultimately resulting in no brood desertion. However, in this study we only have one observation per nest during the provisioning period, so we cannot investigate whether pair coordination is a fixed trait within a pair or if it changes over the provisioning period. However, there is evidence that the degree of pair coordination increases over the provisioning period, especially when parents devote more time to offspring provisioning than other sex-specific tasks, such as brooding, self-foraging (Iserbyt et al., 2017).

The possibility that coordination may reduce sexual conflict has important evolutionary implications. If coordination results in more efficient provisioning and higher offspring fitness, then the payoff for both parents is large in the case of no desertion. In

contrast, if parents fail to reach a level of coordination that benefits the offspring (e.g. because of low parental quality, low behavioural compatibility), it pays to desert the brood. This possibility could be explored in a theoretical model, in which we can test the threshold level of coordination that would cause parents to stay with the current mate or to desert the brood. Parental coordination is an often-overlooked behaviour in studies of parental care. It can be adaptive by reducing sexual conflict and should be investigated both empirically and theoretically to fully understand the persistence of biparental systems.

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