

Published in Behavioural Processes 173 (2020) 104026

<https://doi.org/10.1016/j.beproc.2019.104026>

Sex-specific patterns of minimal compensation of care during and after short term mate removal in biparental blue tits

Mark C. Mainwaring^{a*}, Ian R. Hartley^b

a Division of Biological Sciences, University of Montana, Missoula, MT 59812, USA

b Lancaster Environment Centre, Lancaster University, Lancaster, LA1 4YQ, UK

ABSTRACT

Early theoretical models predicted that over evolutionary timescales, changes in effort by one biparental parent should result in incomplete compensation by the other. Empirical studies, however, report responses ranging from no compensation through to complete compensation which may mean that parents respond to each other's efforts over short time scales, as predicted by some recent theoretical models. Few studies have examined behavioural changes over short time periods which mimic the onset of reduced effort so we removed one blue tit (*Cyanistes caeruleus*) parent for 20 min during nestling provisioning. We then quantified the provisioning rates of both parents for 60 min 'pre-removal', the non-removed partner during the 20 min 'removal' period and both parents for 60 min 'post-removal'. When compared to pre-removal, both sexes reduced their provisioning rates during the removal stage and also during the post-removal stage. There were, however, sex-specific provisioning patterns in the hour after the parent was returned because after females were released, males began provisioning at a relatively high rate and then maintained that rate across the hour after removal whereas after males were released, females began provisioning at a low rate but significantly increased thereafter. There was no long term effect on offspring fitness, which probably reflects the short time parents were removed and so we conclude that parents with biparental care adjust their provisioning rates to successfully overcome very short term decreases in care.

1. Introduction

Biparental care is the most widespread form of care in a range of taxa, including birds in which it occurs in at least 81 per cent of species (Cockburn, 2006). Despite its prevalence, our understanding of the dynamics of biparental care remains incomplete (Lessells, 2012) and it remains unclear to what extent one parent should respond to changes in effort by the other parent. Empirical studies have altered partner effort either through the removal of one parent (e.g. Snoeijs et al., 2005; Smiseth et al., 2005; van Breukelen and Itzkowitz, 2011) or through the manipulation of effort exerted by one parent (e.g. Wright and Cuthill, 1989, 1990a, 1990b; Sanz et al., 2000; Tajima and Nakamura, 2003; Wiebe, 2010; Leclaire et al., 2011). In the later scenario, therefore, both parents are left in situ but one parent is handicapped (Harrison et al., 2009; Lessells, 2012). Meanwhile, studies have experimentally increased partner effort through the playback of offspring begging calls to one of the two parents when they visit the nest (Ottoson et al., 1997; Hinde, 2006; Hinde and Kilner, 2007).

Theoretical models have examined how one parent should adjust their own efforts in relation to changes in the effort exerted by their partner. One of the earliest and most influential models by Houston and Davies (1985) showed that any increase or decrease in effort by one parent should be incompletely compensated for by the other parent. Although the Houston and Davies (1985) model spawned many empirical studies (e.g. Alatalo et al., 1988; Whillans and Falls, 1990; Wolf et al., 1990), it is acknowledged that the Houston and Davies (1985) model refers to long term evolutionary selection pressures on parental behaviours rather than to negotiation rules over short term behavioural time scales (McNamara et al., 1999; Harrison et al., 2009). A negotiation model that examined how partners should respond to changes in effort by their partner also predicted partial compensation (McNamara et al., 2003) and expanded the range of possible responses by showing that over-compensation may be possible (see also Akçay and Roughgarden, 2009). This means that when one parent decreases its own effort, their partner can respond in four ways: they can abandon and thus stop caring, reduce their own effort, increase their own effort or provide the same amount of effort (Jones et al., 2002; Houston et al., 2005; Lessells, 2012; reviewed by Harrison et al., 2009).

Studies manipulating the effort exerted by one parent and examining their partners response have been performed in a wide range of taxa including insects (Rauter and Moore, 2004; Smiseth et al., 2005; Suzuki and Nagano, 2009; Donaldson et al., 2014), fish (Mrowka, 1982; Lavery and Reeb, 1994; van Breukelen and Itzkowitz, 2011) and birds (Griggio and Pilastro, 2007; Lendvai and Chastel, 2008; reviewed by Harrison et al., 2009). Those studies report diverse results with responses ranging from no compensation (Rauter and Moore, 2004; Smiseth et al., 2005; Suzuki and Nagano, 2009), incomplete or partial compensation (Bjornstad and Lifjeld, 2008; Lendvai and Chastel, 2008; Schwagmeyer et al., 2008), complete compensation (Osorno and Székely, 2004; van Breukelen and Itzkowitz, 2011) and perhaps unexpectedly, even over compensation (Griggio and Pilastro, 2007). However, a meta-analysis of 54 studies that had either removed one parent or manipulated the effort exerted by one parent in birds, the most widely studied taxa for this kind of experiment, suggested that most parents partially compensated for changes in effort by their partner (Harrison et al., 2009).

Empirical results largely agree with the Houston and Davies (1985) model and the McNamara et al. (1999, 2003) negotiation models although this does not help explain the wide variety of responses reported in empirical studies (Akçay and Roughgarden, 2009). One possibility is that diversity occurs because the period over which care was manipulated varies (Table 1). Pertinently, the predictions of the Houston and Davies (1985) model differ from the negotiation models of McNamara et al. (1999,

2003) because the former makes predictions about changes over long term timescales in which parents' increased efforts are not open to exploitation by their partner (Lessells, 2012). Further, partial compensation as predicted by the Houston and Davies (1985) model may not be expected in the short term if parents match, rather than compensate for, changes in their partners effort (Hinde, 2006; Johnston and Hinde, 2006; Hinde and Kilner, 2007; Johnston et al., 2014). The Johnston and Hinde (2006) model predicts that parents respond directly and almost immediately to each other's efforts rather than their responses being mediated by offspring, especially when parents negotiate. So whereas the Houston and Davies (1985) model predicts partial compensation should be selected to occur over generations, more recent models (e.g. Johnston and Hinde, 2006) predict shorter term matching within timescales as short as a few minutes under some circumstances because parents respond to change in their partner's efforts in a tit-for-tat manner.

We experimentally removed either male or female blue tit (*Cyanistes caeruleus*) parents for a very short time period during offspring provisioning and quantified the pair's provisioning behaviours prior to the removal, their partner's provisioning behaviour when their mate was removed, and the removed bird and their non-removed partner for one hour after the experimental bird was released. In species with biparental care, the Houston and Davies (1985) model predicts that changes in effort by one parent should be partially compensated for by the other parent in the long term, whilst the Johnstone and Hinde (2006) model also predicts that it should be incompletely compensated for in the short term. We predict first, when males or females are removed during nestling provisioning, their partner will decrease their provisioning rates and will not compensate for their removal, second, that both sexes will react to the removal of their partner in a similar manner because they both provision offspring in a similar manner and third, the removal of focal birds and the absence of compensatory behaviours by their partner will result in nestlings having lower masses at pre-fledging than pairs where neither parent was removed.

2. Methods

2.1 Study area and routine data collection

We studied blue tits breeding in nestboxes within three separate, small (< 30 ha) largely deciduous and occasionally mixed woodlands in Lancashire, northwest England, UK (54°0'N, 02°47'W; Mainwaring et al., 2010) in 2016. From the beginning of April, all nestboxes were checked every three days to determine the day on which the first egg was laid, based on the assumption that they laid one egg per day (Cramp and Perrins, 1993). Nests were checked daily after the sixth egg was laid to establish when incubation began and whilst nests were left largely undisturbed during the incubation period, two days before the predicted hatching date, nests were checked daily for hatching and to quantify hatching success. A total of 63 pairs of blue tits raised offspring through to the age of fledging but of those pairs, 29 pairs had a mate removed and 11 pairs had a male removed, 18 pairs had a female removed and 34 pairs had neither parent removed.

2.2. Parent removal and provisioning rates

When the eldest nestling/s were six to eight days old, one of the adults was caught at 29 (11 male and 18 female parents) nestboxes using a nestbox trap whilst they were provisioning the nestlings. They were marked with a small spot of white correcting fluid on the upper side of the tail so that the male and female parent within each pair could be easily identified on video and immediately released, with the whole procedure taking no longer than two minutes. Then, when the eldest nestling/s were nine to eleven days old, the parental provisioning behaviours were recorded before,

during and after one of the parents was removed for a short time period of twenty minutes. Weather conditions vary considerably over the course of a given day and so if conditions were rainy and cold, we delayed the time at which videos were recorded (Mainwaring and Hartley, 2016b). This meant that in periods of good weather, which comprised periods of sun and warmth as opposed to periods of rain and cold, the video camera was placed on a tripod about 10 m from the nestbox, without actually approaching close to the nestbox itself, in order to film the natural provisioning behaviours of the two parents prior to the removal of one of the parents (Mainwaring and Hartley, 2016a). Then after a period of sixty minutes and with the video still filming, one of the parents was caught at the nestbox using a nestbox trap and held about one hundred meters away from in a bird bag for a period of twenty minutes, which we refer to as the 'removal' stage. All of the removed birds were quiet and thus made no vocalisations during the 'removal' stage of the experiment and that bird was then released back within its territory, within twenty meters of its nestbox. The video camera continued to film the provisioning behaviours of the two parents for another period of sixty minutes in order to quantify their provisioning behaviours after the removed bird was released. The bird marked with correcting fluid was always easy to observe during this period of time and so we are confident that our approach accurately identified the male and female parents at each nestbox.

2.3. Quantifying nestling masses and fledging success

When the eldest nestling/s within broods were fourteen days old, each nestling in all 63 broods (11 = male removed, 18 = female removed, 34 = neither removed) was weighed (± 0.1 g; electronic balance) so that we could quantify both the quantity and quality of offspring at pre-fledging (Mainwaring and Hartley, 2012). The nests were then left undisturbed for 6 days because nest visits during that time may have caused the nestlings to fledge prematurely, and nests were then checked again at day 20 (± 1) to establish fledging success, which was defined as the number of fledglings from each nestbox. 2.4. Statistical analyses Data were analysed using the SPSS v23.0 (SPSS, Chicago, IL, USA) statistical package. The effect of mate removal on parental provisioning patterns was analysed using a Linear Mixed Model and for this section of the analyses, we used parental provisioning rates per twenty minute time intervals to examine fine-scale patterns of provisioning throughout the 'before', 'during' and 'after' stages of mate removal. The dependent variable was 'provisioning rate' (number of feeds per twenty minute period) and 'removal stage' (before, during and after removal), 'sex' (male or female) and 'mate removed' (yes or no) were explanatory factors and 'brood size' and 'first egg date' (days after 1 st April) were explanatory covariates, whilst nest identity was included as a random effect to control for the non-independence of two parents provisioning at the same nestboxes. Each of those main terms, and all of their twoway and three-way interaction terms, were initially entered into full models but when the P value of terms were not significant, they were dropped from the model until only those fixed terms which were significant ($P < 0.05$), or were involved in a significant two- and threeway interaction term, were retained, thereby yielding the final minimal model (Crawley, 1993).

To examine the effects of mate removal on the quantity and quality of nestlings raised, two different models were used. The first model examined the effects of mate removal on the quality of nestlings raised was a General Linear model with 'mean brood mass at day 14' as the dependent variable, and removal status (male removed, female removed, no mate removed) as an explanatory factorial variable and first egg date (days after 1 st April) and brood size as explanatory covariates. Fledging success data were arcsine square root transformed as appropriate and the second model was a Generalised Linear Model with a poisson error structure and had 'fledging success' as the dependent variable and had the same explanatory variables as the first model immediately above. In both

models, each of the main terms, and all of their two-way interaction terms, were entered into full initial models before those models were then simplified following the procedures outlined in the paragraph immediately above (Crawley, 1993). All statistical tests were two-tailed, means are presented ± 1 standard error and a critical P-value of 0.05 was applied throughout.

3. Results

The provisioning rates of blue tit pairs varied in relation to removal stage ($P < 0.001$), with post-hoc Tukey tests indicating they were higher 'before' than both 'during' and 'after' removal, with provisioning rates being similar 'during' and 'after' removal (Figs. 1 and 2; Table 2). This means that blue tits reduced their provisioning rates in response to the reduced amount of care provided by their partner. The provisioning rates of pairs were also positively correlated with brood sizes, but unrelated to first egg dates (Table 2). Meanwhile, only three of the two and three-way interaction terms were significant and they all included the term 'sex' which indicated sex-specific responses to the experimental removal of their mates. Provisioning rates varied in a sex-specific manner ($P = 0.036$) and a highly significant two-way interaction term between 'sex' and 'mate removed' ($P < 0.001$) in addition to a highly significant three-way interaction term between 'removal stage', 'sex' and 'mate removed' ($P < 0.001$) demonstrated sex-specific responses to partners being removed. Specifically, there were sex-specific provisioning patterns in the hour after the mate was returned because after females were released, males began provisioning at a relatively high rate and maintained that across the hour after removal whereas after males were released, females initially provisioned at a low rate but significantly increased thereafter. Provisioning rates never varied between the three twenty minute periods 'before' and the one twenty minute period 'during' removal but post-hoc Tukey tests showed sex-specific provisioning patterns after experimental birds were released. After females were released back into their territory, their male partners immediately began feeding at a relatively high rate which continued unchanged for the whole hour, whilst when males were released after having been removed, females initially fed at a very low rate but significantly increased their provisioning rates over the course of the next hour (Figs. 1 and 2; Table 2). Finally, a highly significant three-way interaction term between 'sex', 'mate removed' and 'brood size' ($P < 0.001$) demonstrated that females provisioned larger broods more frequently when their mate was removed than males did when their mate was removed. The mean mass of the nestlings at pre-fledging was not influenced by removal stage, first egg dates or brood sizes at pre-fledging or any of their two-way interaction terms. Meanwhile, the fledging success of broods was, unsurprisingly, positively correlated with their brood sizes at pre-fledging (Table 3) but otherwise was not influenced by removal stage, first egg dates or any other of their two-way interaction terms.

4. Discussion

The main findings of this study were that both male and female blue tit parents reduced their provisioning rates both during the short twenty minute time period whilst their partner was removed and also during the one hour time period after the removed bird was released. Nonremoved parents therefore responded to short term reductions in care by their partner by providing a matching response, as the recent negotiation models of Johnston and Hinde (2006) predict because each partner makes real time decisions as to how much care to provide based on their mate's investment. There were, however, sex-specific patterns of provisioning after the removed bird was released because after females were removed, post-hoc Tukey tests revealed that

their male partners immediately began feeding at a relatively high rate which continued unchanged for the whole hour. After males were released, meanwhile, post-hoc Tukey tests revealed that females initially fed at a very low rate but increased their provisioning rates over the course of the following hour. There was, however, no variation in nestling masses at pre-fledging or fledging success when compared to broods where neither parent was removed.

It is prudent, however, to consider how our methodological approach may have influenced the findings of our study. In this regard, it is important to remember that our experiment included the catching of parents at the nestboxes prior to their experimental removal and so it is possible that our activities had an effect on parental provisioning by both the removed bird after they were released and also by their nonremoved partner both during and after the removal stage of the experiment. More specifically, our experimental approach means that we are unable to explicitly determine whether any changes in parental effort were due to the effect of a change in the partner's behaviour or as a result of human disturbance when erecting the video camera or catching one of the parent birds. The absence of a control group in which the birds were not disturbed by humans at all mean that we are unable to distinguish between these two possibilities. In this way, our methodological approach may have influenced the findings and it would be prudent to view our results in light of these potential influences (Schlicht et al., 2015).

Neither male nor female blue tits compensated for the short term removal of their partner whilst they were removed for twenty minutes and during the hour after the removed bird was released. This broadly disagrees with the predictions of both the Houston and Davies (1985) model and the more recent McNamara et al. (1999, 2003) negotiation models. This is seemingly quite surprising given that whilst the Houston and Davies (1985) model predicts that changes in effort by one partner should result in incomplete compensation by the other partner, the negotiation models of McNamara et al. (1999, 2003) rigidly predict an even smaller degree of compensation because the efforts of the nonremoved parent can be exploited by their partner (Lessells, 2012). The idea that incomplete compensation may be expected over longer, rather than shorter, time scales is supported by more recent theoretical models and empirical studies of great tits (*Parus major*) which suggest that biparental parents match, rather than compensate, for changes in their partners effort over extremely short time frames such as within twenty minute periods of time (Hinde, 2006; Johnston and Hinde, 2006; Hinde and Kilner, 2007; Johnston et al., 2014). In agreement with this idea, blue tit parents of both sexes have been shown to exhibit incomplete compensation when their partner is removed over relatively long time periods (Sasvári, 1986) and therefore, not compensating is only likely to be adaptive over short time periods in an effort to avoid their own efforts being exploited by their partner. Blue tit and great tit parents both therefore appear to match each other's workloads over relatively short time periods which is perhaps unsurprising given that they are roughly equally invested in the brood that they are jointly provisioning.

A decrease in effort by the non-removed partner during partner removal, otherwise known as partner matching, has been reported in taxa other than birds. In beetles, males but not females, compensate for the experimental removal of their partner (Rauter and Moore, 2004; Smiseth et al., 2005; Suzuki and Nagano, 2009) although the reasons why individuals do not compensate for a reduction in their partner's efforts in the short term remains unclear. It may simply be that individuals are already working close to capacity but this seems unlikely as no compensation often consists of a reduction in effort. Alternatively, the 'sealed-bid' model of biparental care suggests that parents use a fixed amount of effort in an effort to reduce the possibility of their partner exploited them. More recently, the emphasis has shifted toward negotiation over parental effort and empirical support for the active negotiation of effort between parents comes from a mate removal study of

house sparrows (*Passer domesticus*) (Lendvai et al., 2009) and studies of other passerine birds which show that parents alternated visits more than would be expected by chance (e.g. Johnston et al., 2014; Bebbington and Hatchwell, 2016). Provisioning rates in the Johnston et al. (2014) study increased and decreased after the increase and decrease of their partner's provisioning rates, respectively and because visit-to-visit variation in the begging intensity of nestlings did not vary, then parental provisioning rules appeared to be determined by variation in their partners efforts and not by the needs of their offspring (Johnston et al., 2014). Species with biparental care may, therefore, simply be negotiating their own provisioning rules over short time frames via a relatively simple form of reciprocity.

Whilst we are unable to distinguish whether these patterns were caused by the removal of one parent or the human disturbance during the process of the capture and release of one parent (Schlicht et al., 2015), sex differences after removal nevertheless existed. This agrees with recent research which suggests that biparental pairs closely match the workload of their partner (Hinde, 2006) because whilst females matched male workloads, males did not. The reasons for the existence of sex-specific provisioning patterns following the removal of one parent are unclear but they may have occurred because females took more notice of male work rates than vice versa. Alternatively, a degree of sex-specific task specialisation may explain sex-specific responses, as highlighted in response to partner removal in beetles (Rauter and Moore, 2004; Smiseth et al., 2005; Suzuki and Nagano, 2009) where sex-specific differences exist in relation to the anti-microbial activity of anal exudates used to protect carcasses in burying beetles (*Nicrophorus vespilloides*) (Cotter and Kilner, 2010). Convict cichlid (*Amatitlania nigrofasciata*) males fully compensate for female removal whereas females do not (van Breukelen and Itzkowitz, 2011) and it was concluded that females were simply unable to fully compensate for male removal. The removal of male Eurasian treecreepers (*Certhia familiaris*) changed the female's foraging niche and it was suggested that such adaptive changes influence sex-specific responses to partner efforts (Aho et al., 1997). Each of these possibilities are plausible causes of sex-specific responses to partner removal in birds, and possibly other taxa as well, although further research is needed to elucidate the exact mechanisms underlying sex-specific responses to changes in partner effort in species with biparental care.

The short term removal of one parent of either sex did not affect the mass of nestlings at pre-fledging or the amount of fledglings. This suggests that parents with biparental care can successfully overcome short term reductions in care provided by either one or both parents by rapidly adjusting their provisioning rates afterwards. These findings agree with a study of blue tits which found that pairs simultaneously gradually resumed provisioning activity and reduced nest defence activities after an experimental increase in the perceived risk of predation and after the risk of predation had diminished, they increased their provisioning rates above normal to compensate for the short term disruption to their provisioning behaviours (Mutzel et al., 2013). This suggests that parents negotiate their respective workloads so that after the removed bird was returned in our study, it is likely that the pair quickly overcame that decrease in care to raise their nestlings. It is important to distinguish between long term and short term parental removal because whilst male removal over long time periods in birds usually results in lower offspring survival (Bart and Tornes, 1989; Lynn and Wingfield, 2003; Bjornstad and Lifjeld, 2008; Table 1) temporary removals such as in our experiment do not generally affect offspring quantity and quality (Duckworth, 1992; Table 1). Whilst it is prudent to consider that the absence of any discernible effects on offspring quantity and quality may have been masked by compensatory behaviours by the parents, as shown in a study of black-legged kittiwakes (*Rissa tridactyla*) (Leclaire et al., 2011), the absence of an effect is probably unsurprising. In small passerine birds such as blue tits which are short lived and in Great Britain, single-brooded, this means the nestlings in any given brood represents a significant proportion of their potential

lifetime reproductive success which presumably therefore makes it adaptive to rapidly overcome short term disruptions to provisioning.

We conclude that it is adaptive for parents with biparental care to rapidly overcome short term decreases in care by one parent to maximise their reproductive success. Two areas of research deserve further attention and in this regard, first, it would be interesting to quantify how long it took for both parents to resume normal provisioning rates either after the removal of one partner or some other kind of incident such as an unsuccessful predation event to examine temporal trade-offs between various parental care behaviours. Second, further research is needed to examine how closely parents match each other's efforts to examine the limit to which the absence of one parent influences the other because absences by one parent may occur due to the stochastic nature of finding food in adverse weather conditions, rather than negotiation rules alone and so examining how weather conditions influence provisioning rules may prove insightful.

Author contributions

M.C.M. and I.R.H. designed the study, performed the fieldwork, analysed the data and wrote the paper.

Acknowledgements

We thank Stuart Sharp for useful discussions.

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Fig 1. The mean \pm standard error male, female and total blue tit provisioning rates before (T1-T3), during (T4) and after (T5-T7) the female was removed for twenty minutes when the eldest nestling/s were ten days old.

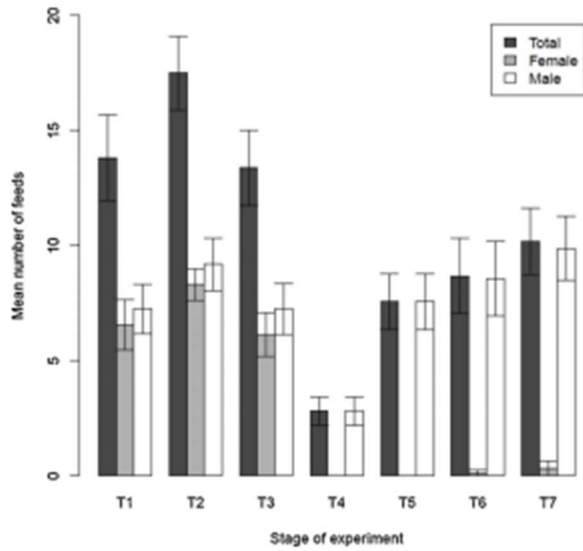


Fig 2. The mean \pm standard error male, female and total blue tit provisioning rates before (T1-T3), during (T4) and after (T5-T7) the male was removed for twenty minutes when the eldest nestling/s were ten days old.

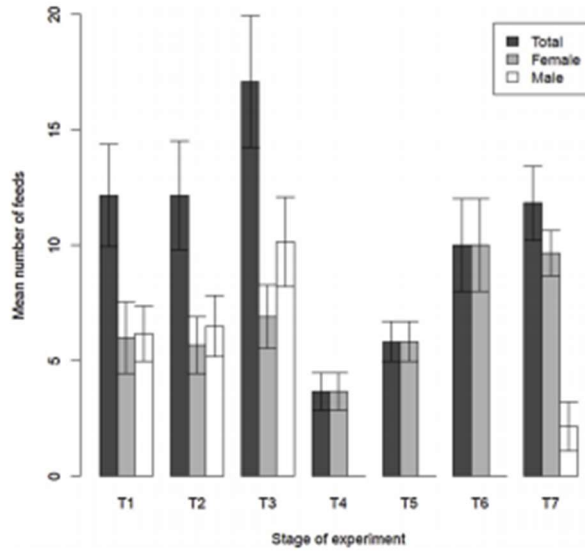


Table 1

Species	Sex removed	When removed and duration ^a	Partner response	Fitness consequences	Reference
American kestrel <i>Nihoa sparverius</i>	Male	During incubation onwards	Courship to attract a new partner	None reported	Bowman and Bird, 1987
American kestrel <i>Nihoa sparverius</i>	Male	During incubation onwards	Courship to attract a new partner	None reported	Bowman and Bird, 1987
Blue tit <i>Cyanistes caeruleus</i>	Male	At various stages of nestling provisioning onwards	Increased provisioning rates	Reduced fledging success	Susvid, 1986
Blue tit <i>Cyanistes caeruleus</i>	Female	At various stages of nestling provisioning onwards	Increased provisioning rates	Reduced fledging success	Susvid, 1986
Blue tit <i>Cyanistes caeruleus</i>	Male	Day 8 of nestling period for 20 minutes	Reduced provisioning rates	None reported	This study
Blue tit <i>Cyanistes caeruleus</i>	Female	Day 8 of nestling period for 20 minutes	Reduced provisioning rates	None reported	This study
Blue tit <i>Cyanistes caeruleus</i>	Male	Day 7 of nestling period for about 6 hours	Increased provisioning rates	None reported	Smith and Amundson, 2000
Dark-eyed junco <i>Anco hyemalis</i>	Male	When eggs hatched onwards	Continued to feed nestlings	Reduced fledging success	Wolf et al., 1988
Dark-eyed junco <i>Anco hyemalis</i>	Male	When eggs hatched onwards	Increased provisioning rate	Reduced fledging success	Wolf et al., 1990
Dark-eyed junco <i>Anco hyemalis</i>	Male	When eggs hatched onwards	Increased provisioning rate	Reduced fledging success	Wolf et al., 1991
Great tit <i>Parus major</i>	Male	At various stages of nestling provisioning onwards	Increased provisioning rates	Reduced fledging success	Susvid, 1986
Great tit <i>Parus major</i>	Female	At various stages of nestling provisioning onwards	Increased provisioning rates	Reduced fledging success	Susvid, 1986
Great reed warbler <i>Acrocephalus arundinaceus</i>	Male	Day 8 of nestling period onwards	No change in nest defence behaviours	None reported	Trška and Grim, 2013
Great reed warbler <i>Acrocephalus arundinaceus</i>	Female	Day 8 of nestling period onwards	Decreased nest defence behaviours	None reported	Trška and Grim, 2013
House sparrow <i>Passer domesticus</i>	Male	Day 7 of nestling period for 48 hours	Increased provisioning rate	Nestlings in worse condition	Lendvai and Chastel, 2008
House sparrow <i>Passer domesticus</i>	Female	Day 7 of nestling period for 48 hours	Moderately increased provisioning rates	None reported	Lendvai et al., 2009
House sparrow <i>Passer domesticus</i>	Male	Day 7 of nestling period for 30 minutes	Increased provisioning rates	None reported	Lendvai et al., 2009
Kestrel plover <i>Charadrius alexandrinus</i>	Male	Shortly after hatching onwards	Continued to raise chicks	Reduced chick survival	Selby and Cuthill, 1999
Kestrel plover <i>Charadrius alexandrinus</i>	Female	Shortly after hatching onwards	Continued to raise chicks	Reduced chick survival	Selby and Cuthill, 1999
Kestrel plover <i>Charadrius alexandrinus</i>	Male	During incubation for about 1.6 days	No observed changes	None reported	Kozsolyai et al., 2003
Kestrel plover <i>Charadrius alexandrinus</i>	Female	During incubation for about 1.6 days	Increased incubation	None reported	Kozsolyai et al., 2003
Killdeer <i>Charadrius vociferus</i>	Male	Late incubation onwards	Abandoned eggs which never hatched	Brooding failure	Brunton, 1988
Killdeer <i>Charadrius vociferus</i>	Female	Late incubation onwards	Continued to incubate eggs and raise chicks	None reported	Brunton, 1988
Lesser snow goose <i>Anser caerulescens</i>	Male	During early incubation onwards	None reported	None reported	Martin et al., 1985
Orange-tufted sunbird <i>Nectarinia osea</i>	Male	Shortly after hatching onwards	Increased provisioning rate	Lower post-fledging survival	Markman et al., 1996
Magpie <i>Pica pica</i>	Male	Varied between egg laying and nestling provisioning onwards	Reduced provisioning rates	Complete brooding failure	Dunn and Hanson, 1989
Pied flycatcher <i>Recurvulus hypoleucos</i>	Male	Day when the first egg was laid onwards	Reduced provisioning rates	Reduced fledging success	Altshuler et al., 1982
Pied flycatcher <i>Recurvulus hypoleucos</i>	Female	Days 6-9 of nestling period onwards	Decreased initial, but increased later, provisioning rates	None reported	Szere et al., 1995
Red-winged blackbird <i>Agelaius phoeniceus</i>	Female	Early during the nestling period onwards	Increased provisioning rates	None reported	Whittingham et al., 1994
Red-winged blackbird <i>Agelaius phoeniceus</i>	Male	Late during the nestling period onwards	Increased provisioning rates	None reported	Whittingham et al., 1994
Red warbler <i>Acrocephalus scirpaceus</i>	Female	During incubation onwards	Increased provisioning rates	None reported	Dackworth, 1992
Savannah sparrow <i>Passerculus sandwichensis</i>	Male	Shortly after eggs hatched onwards	Increased provisioning rates	None reported	Froemer-Gallant, 1998
Savannah sparrow <i>Passerculus sandwichensis</i>	Female	Varied between late incubation and after hatching onwards	Increased provisioning rates	Lower post-fledging survival	Gorenlov and Post, 1985
Tree swallow <i>Ichtyophaga borealis</i>	Male	Early during the nestling period onwards	Increased provisioning rates	Lower fledging success	Whittingham et al., 1994
Tree swallow <i>Ichtyophaga borealis</i>	Female	Varied between incubation and nestling provisioning onwards	Increased provisioning rates	None reported	Dunn and Hanson, 1992
Willow warbler <i>Phylloscopus collybita</i>	Male	Start of egg laying and day 7 of nestling period onwards	Increased provisioning rates	Reduced nestling growth	Biomstad and Lifjeld, 2008
Wood thrush <i>Aix sponsa</i>	Male	Early during incubation onwards	None reported	Fewer second broods	Mastore and Herpp, 1998

^a Onwards refers to birds being removed for the remainder of the non-reproductive event

Table 2. Summary of a Linear Mixed Model examining male, female and total blue tit provisioning rates when males or females were removed. The dependent variable was 'provisioning rate' (number of feeds per twenty minute period) and 'removal stage' (before, during and after removal), 'sex' (male or female) and 'mate removed' (yes or no) were explanatory factors and 'brood size' and 'first egg date' (days after 1st April) were explanatory covariates, whilst nest identity was a random effect.

Fixed effects	d.f.	F-value	P value
Removal stage	2,345	18.817	< 0.001
Sex	1,345	4.448	0.036
Mate removed	1,25	0.251	0.62
First egg date	1,25	0.24	0.628
Brood size	1,25	16.18	< 0.001
Sex x mate removed	1,335	39.74	< 0.001
Removal stage x sex x mate removed	1,323	84.734	< 0.001
Sex x mate removed x brood size	1,323	13.844	< 0.001

Table 3. Summary of General Linear Models examining mean brood mass at day 14 and fledging success of blue tits when male and female parents were removed. The two models had 'mean brood mass at day 14' and 'fledging success' as dependent variables and had removal status (male removed, female removed, no mate removed) as an explanatory factorial variable and first egg date (days after 1 st April) and brood size as explanatory covariate variables.

Breeding variable	Fixed effects	d.f.	F-value	P value
Nestling mass	Removal stage	1	0.475	0.624
	First egg date	1	0.286	0.595
	Brood size	1	1.576	0.215
Fledging success	Removal stage	1	1.824	0.219
	First egg date	1	1.725	0.318
	Brood size	1	24.385	< 0.001