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ORIGINAL ARTICLE

Nest-site interference competition with House Sparrows affects breeding success and parental care in Great Tits

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Abstract
Although interspecific competition is suggested to be one of the major forces dictating community structure, interspecific interference competition for nest sites in birds has been reported mainly from observational studies. Here, we asked whether interference by the larger House Sparrow (*Passer domesticus*) could reduce breeding success and parental behavior in the smaller Great Tit (*Parus major*) following clutch completion, by experimentally allowing House Sparrows to access half of the Great Tit nest boxes. Significantly more tit pairs failed to raise young in nest boxes that House Sparrows were able to enter during their breeding period compared to those that were not able to do so, because House Sparrows usurped 77.8% of the Great Tit nests. Great Tits also increased the duration of nest defense in the presence of House Sparrows. As the outcome of interference competition may lead to breeding failure, birds should necessarily evolve ways to avoid nest competitors either by selecting nests that restrict access to their larger competitors and/or by initiating breeding earlier. Conservation efforts should be directed toward attaching a metal restrictor plate around the entrance of nest boxes to prevent woodpeckers from enlarging the entrance and larger species from entering nests.

Keywords Interspecific interactions · Nest failure · Parental behavior · Community structure · Nest box · Usurpation

Zusammenfassung
Konkurrenz um Nistplätze mit dem Haussperling beeinträchtigt den Bruterfolg und die elterliche Brutpflege von Kohlmeisen
Obwohl zwischenartliche Konkurrenz angeblich eine der wichtigsten treibenden Kräfte hinter der Gemeinschaftsstruktur ist, wurde zwischenartliche Konkurrenz um Nistplätze bei Vögeln bislang in erster Linie nur mit reinen Beobachtungen beschrieben. In dieser Untersuchung prüften wir, ob Störungen durch den Haussperling (*Passer domesticus*) den Bruterfolg und die Brutpflege von Kohlmeisen (*Parus major*) beeinträchtigen können. Nach Komplettierung der Gelege der Kohlmeisen ermöglichten wir in einem Experiment den Haussperlingen Zugang zur Hälfte der vorhandenen Meisenkästen. In diesen Nestern waren signifikant mehr Meisenpaare nicht in der Lage, ihre Jungen aufzuziehen, als in Nestern ohne Zugang von Haussperlingen, weil die Haussperlinge 77,8% dieser Nistkästen übernahmen. Waren Haussperlinge in der Nähe, verbrachten die Kohlmeisen auch mehr Zeit mit der Verteidigung ihrer Gelege. Da diese Art der Konkurrenz zu Brut-Misserfolgen

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führen kann, sollten Vögel Methoden entwickeln, solche Nestkonkurrenten zu vermeiden, entweder durch die Auswahl von Nisthöhlen, die es ihren größeren Konkurrenten unmöglich macht einzudringen und/oder durch einen früheren Brutbeginn. Um zu vermeiden, dass Spechte das Flugloch erweitern, und so größere Arten die Höhlen übernehmen, können Metallplatten um die Einfluglöcher angebracht werden.

Introduction

Interspecific competition plays a major role in shaping ecological communities (Schoener 1983; Connell 1983; Roughgarden 1983; Schluter 2000; Dayan and Simberloff 2005) and is mainly divided into exploitation competition and interference competition (Case and Gilpin 1974). Exploitation competition occurs indirectly through the consumption of a limited resource, which then becomes unavailable for other individuals (Minot and Perrins 1986). Interference competition occurs when individuals prevent access to a limited resource through direct negative interactions such as aggressive acts (Wiens 1992). Even though interspecific competition has been suggested to be common in nature in a variety of taxa from invertebrates to vertebrates, most theories of interspecific competition have focused mainly on exploitation competition (Amarasekare 2002; Dhondt 2011), mainly due to the difficulty in designing studies specifically directed at interference competition.

Cavity-nesting birds offer an excellent model system to study the effect of interspecific competition, particularly in secondary cavity-breeding species that use nest boxes (Lambrechts et al. 2010). Using nest boxes in field experiments allows researchers to measure the effect of potentially competing species on breeding success by means of manipulating species density when nest cavities are limited (Dhondt 2011). Most studies that have used cavity-nesting birds to examine interspecific competition have produced mainly indirect evidence that such competition occurs (Newton 1998; Dhondt 2011), while most of the experimental studies on nest-site competition were designed to test for exploitation competition (Dhondt and Eyckerman 1980; Strubbe and Matthysen 2009; Charter et al. 2013, 2016) and fewer have examined the effect of interference competition (Van Balen et al. 1982; Wiebe 2016). Several studies have provided evidence of the existence of interference competition, for example between resident Great Tits (*Parus major*) and migratory Pied Flycatchers (*Ficedula hypoleuca*), in which fighting over nest holes increased adult mortality in the subordinate Pied Flycatchers (Slagsvold 1975; Winge and Järvi 1988; Meek and Robertson 1994; Merilä and Wiggins 1995). Additional studies have found anecdotal evidence that interspecific nest usurpation reduces the breeding success of cavity-nesting birds (Charter et al. 2013, 2016; Frei et al. 2015).

The behavior of birds should necessarily change in the presence of nest-site competitors, similar to nest defense against predators (Martin et al. 2000), because interference nest-site competition can also result in complete nest failure. To avoid competition, small bird species prefer to breed in cavities with a smaller entrance that restricts access to the larger competitor bird species, but nonetheless prefer larger entrances when they are alone (Dhondt and Eyckerman 1980; Kempenaers and Dhondt 1991; Charter et al. 2010a, 2013). Cavity breeders were found to invest more time in protecting nests in the presence of potential nest-site competitors than non-nest-site competitors, even though both types may also compete for food (Král and Bicík 1992; Krist 2004; Pearce et al. 2011). Additional studies on nest-site competition using model species that only compete for one resource will help to tease apart the effect of each of the resources (e.g., food and nest site) that shape these competitive interactions.

Here, we used a system of two different-sized very common resident secondary cavity-breeding passerines: Great Tits [mean weight 16.0 g (Israeli Bird Ringing Center)] and House Sparrows [mean weight 31.1 g (Israeli Bird Ringing Center)], that compete for nest sites but not for food. Great Tits are mainly insectivorous while House Sparrows are largely granivorous. Even though House Sparrows include insects in the first few days' diet of their nestlings (Cordero and Summers-Smith 1993), the two species forage in different places: Great Tits forage mainly on bushes and trees (Shirihai 1996), while House Sparrows forage mainly on the ground (Summers-Smith 1967). Great Tits start to breed almost 2 months before House Sparrows and unlike in Europe, House Sparrows in Israel do not use cavities to roost in the winter but, rather, communal roosts, mainly in trees. Consequently, nest-site competition should be more intense after sparrows initiate breeding. For example, Charter et al. (2013) found that the smaller Great Tits bred less in nest boxes with entrances that House Sparrows could enter, during the second part of the Great Tit breeding season, due to exploitation competition. Even though that study found anecdotal evidence of House Sparrows usurping Great Tit nests, experimental studies are needed to determine whether Great Tit breeding is reduced not only due to exploitation competition (lack of nest sites) but also to interference competition.

Using a nest manipulation design by changing the entrance size of nest boxes, we investigated whether interference competition by the larger House Sparrows would reduce the breeding success of the smaller Great Tits both before and after House Sparrows had initiated breeding. In addition, we examined whether the presence of House Sparrows affected the parental care levels of the Great Tits. Since

House Sparrows are larger than Great Tits and have been observed to usurp nests, we predicted that Great Tit breeding success would be lower in nest cavities that House Sparrows could enter but only after the sparrows had initiated breeding. Just as in the presence of other predators, we further predicted that Great Tits would increase nest defense levels in the presence of sparrows.

Methods

Study sites

The study was conducted during the 2012 breeding season in two sites, Kibbutz Geva 32°33′59″N, 35°22′19″E, and Kibbutz Sde Eliyahu 32°26′30″N, 35°30′49″E in the north-east of Israel in areas with small buildings no higher than two stories, with lawns, ornamental trees and irrigated vegetation, and surrounded by irrigated agricultural fields.

Experimental setup

One hundred and seventy-two nest boxes were installed 1 year prior to the beginning of the experiment. The nest boxes were constructed from 1.7-cm-thick birch plywood (external dimension of 15 cm × 15 cm × 24 cm, width × length × height) with an entrance hole of 50 mm, and were attached to trees at a height of 1.5–2.0 m. Small-entrance (28 mm in diameter) metal restrictor plates (Dhondt 2011) were placed over the entrances of all the nest boxes in order to allow access to Great Tits while preventing access to all the other larger secondary cavity breeders. Great Tits readily breed in 28-mm entrances (Charter et al. 2013), whereas this size restricts entrance to House Sparrows, which have been found to need a minimum 29-mm entrance in Israel (Charter et al. 2010b). The subspecies of Great Tit in Israel (*Parus major terraesanctae*) is smaller than the subspecies in Europe (*Parus major major*) and therefore breeds in smaller entrance nest boxes than in Europe (Hedblom and Söderström 2012).

After the Great Tits finished laying their clutch and started to incubate, the 28-mm metal restrictor plates were replaced in the following two treatments. Half of the metal restrictor plates were replaced by large-entrance metal plates (39 mm in diameter), which were large enough for House Sparrows to enter, while the other half of the metal plates were replaced with identical small-entrance metal plates (28 mm) that restricted access to House Sparrows. We switched metal plates in the second treatment (small- to small-entrance metal plates) in order to control for the effect of any disturbance during the experimental manipulation of the plates. As nest boxes had an internal entrance size of 50 mm in diameter, the internal height from the bottom of the nest boxes to the internal entrance was identical in all treatments. The replacement of the two different sized metal restrictor plates was alternated starting from the first laying pair, so that the first metal plate was changed from small to small, the second from small to large, the third from small to small, etc. The large-entrance metal restrictor plate size (39 mm) was selected because this is large enough for House Sparrows to enter but prevents access by even larger secondary cavity-nesting species such as the Scops Owl (*Otus scops*), Hoopoe (*Upupa epops*), Common Myna (*Acridotheres tristis*), and Rose-ringed Parakeet (*Psittacula krameri*) (Charter et al. 2010a, 2013, 2016).

Restrictor plates were replaced only after the Great Tits had finished laying clutches in order to eliminate any potential effect of exploitation competition by House Sparrows (i.e., occupying nest boxes before Great Tits). Furthermore, in comparison to Charter et al. (2013) who studied nest box selection of different sized entrances, this experimental design restricted the ability of the Great Tits to choose a nest box according to its entrance size. Finally, in our study the Syrian Woodpecker (*Dendrocopos syriacus*) often enlarges the entrances of nest boxes and natural nesting cavities (Charter et al. 2010b). Thus, the artificial change in nest entrance diameter in this study is an ecologically relevant approach. The findings of our study are expected to help conservation biologists to decide whether to add a metal ring to the entrance of each nest box to prevent woodpeckers and other primary cavity nesters from enlarging the entrances to these nests.

Breeding success

In order to determine nest box occupation and be able to replace the restrictor plates in time, all the nest boxes were visited (by A. G.) every other day, from 1 January to 30 June 30 2012. Clutch size (number of eggs) and the number of young fledged per breeding attempt (number of young at banding, at 12–14 days of age, minus any dead young found in the box after fledging) were recorded for every breeding attempt. Nestling age during banding and behavioral observations were determined by backdating from the date the first eggs hatched. As expected, due to the close geographic proximity of the two sites, clutch size ($U = 77.5$, $P = 0.78$), brood size ($U = 72.5$, $P = 0.61$) and number fledged ($U = 83.5$, $P = 0.98$) were similar, and the data were therefore pooled. The causes for failure by unsuccessful pairs (pairs that did not fledge any young) were noted: abandonment (when nestlings were found dead inside the nest but were not injured or killed; all nestlings were the same age); predation (when nestlings had disappeared from the nest); and House Sparrow usurpation (House Sparrows expelled Great Tits and built a nest over a Great Tit nest).

Since nest-site competition of our study sites is seasonally asymmetric, according to the later date when House

Sparrows initiate breeding (Charter et al. 2013), we divided the breeding season into two different parts: the first part (before the House Sparrow breeding season) comprised those Great Tit pairs that laid eggs from 1 January to 27 February; and the second part (during House Sparrow breeding) comprised those that laid eggs from February to 1 April. The first of April was the date when the Great Tits started to lay second clutches. To avoid pseudoreplication, only the first clutches of each tit pair (adults were color banded) were included in the experiment.

Behavior in the presence of a competitor

Parental behavior by Great Tits, around the nest box and on the tree where the nest box was located, was studied for 1 h when the nestlings were 12 days old. The behavior of adults was recorded using both a Bushnell 10 × 50-mm Powerview wide-angle binocular and a Panasonic HDC-SD800 video camera placed within 3 m from the nest, which recorded continuously in Advanced Video Coding High Definition 1920 × 1080/24p mode. The videos were analyzed using Adobe Premiere Pro CS5.5 and the audio files were analyzed using Audiofile Triumph 2.0. The duration of each type of behavior was measured in milliseconds and later was rounded off to the nearest second.

A visit by a Great Tit was defined as an event in which one of the parents arrived at the nest tree. During the observations, data were collected on Great Tit nest defense in nest boxes where House Sparrows were present (on the tree hosting the nest boxes during the observation period) or absent (no House Sparrows were seen). We recorded the total number of visits and the duration per visit (seconds) that the parents were present on the nesting tree, the time that the parents spent inside the nest box, and the time spent making alarm calls. At the end of each behavioral observation, nestlings were ringed with aluminum identification ring.

Statistical analyses

As the data were not normally distributed, we used the Mann–Whitney U-test and Fisher's exact test for independent samples. All statistical tests were two-tailed and P-values < 0.05 are considered significant. Statistical analyses were performed using SPSS 23.

Results

Breeding success

Great Tit clutch size was similar between pairs breeding in the small-entrance and large-entrance nest boxes both before (small, median = 7 eggs, $n = 9$ clutches, range 4–9 eggs vs. large, median = 7 eggs, $n = 8$ clutches, range 6–9 eggs) ($U = 33.5$, $P = 0.82$), and after House Sparrows initiated breeding (small, median = 7 eggs, $n = 8$ clutches, range 4–8 eggs vs. large, median = 6 eggs, $n = 9$ clutches, range 4–8 eggs) ($U = 24.5$, $P = 0.28$). There was no difference in the number of young Great Tits fledged by pairs breeding in small-entrance (median = 6 nestlings, $n = 8$ broods, range 0–8 nestlings) and large-entrance nest box treatments (median = 6 nestlings, $n = 9$ broods, range 0–9 nestlings) ($U = 23.5$, $P = 0.24$) before the House Sparrows initiated breeding. However, after House Sparrows started to breed, the Great Tit breeding success was significantly higher in pairs breeding in the small (median = 4.5 nestlings, $n = 9$ broods, range 0–6 nestlings) than in the large-entrance (median = 0.0 nestlings, $n = 8$ broods, range 0–5 nestlings) nest box treatments ($U = 13.5$, $P = 0.027$).

The number of young fledging was lower in Great Tit pairs breeding in the large- vs. small-entrance treatments due to significantly more pairs failing completely (did not fledge any young) in the former (Fisher exact test $P < 0.05$; Fig. 1). Eight out of the nine Great Tit pairs that had bred in the large-entrance nest treatment failed to raise any young, with House Sparrows usurping seven of the nests. In four out of the seven usurped Great Tit nests in the large-entrance nest boxes that failed during incubation, House Sparrows had built their nests over the existing Great Tit nests. House Sparrows usurped an additional three Great Tit nests with nestlings, killing the nestlings and building nests above them. In comparison, before House Sparrows started to breed, the percentage of Great Tit pairs that failed to fledge young was similar between the large- and small-entrance treatments (Fisher exact test $P = 1.00$; Fig. 1) and none of the large-entrance nest boxes were usurped by House

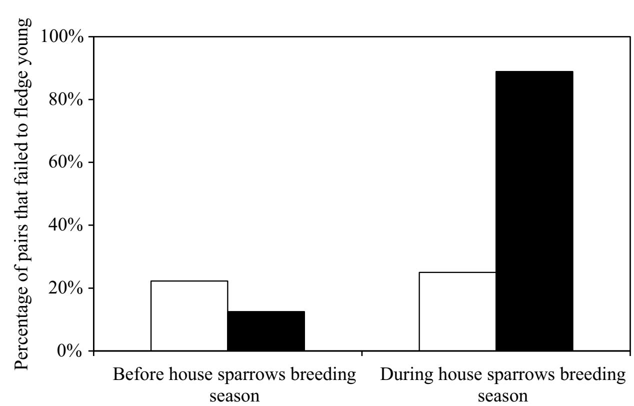

Fig. 1 Comparison between the percentage of Great Tit pairs that failed to breed in the small- (white) vs. the large-entrance (black) treatments, both before House Sparrows initiated breeding (1 January–27 February) ($n_{small} = 9$ tit breeding pairs, $n_{large} = 8$ tit breeding pairs) and after they began to do so (28 February–1 April) ($n_{small} = 8$ tit breeding pairs, $n_{large} = 9$ tit breeding pairs)

Sparrows. Before the sparrows bred, two small-entrance nest boxes with nestlings were abandoned and the nestlings of one pair breeding in a large-entrance nest boxes were predated. During the breeding period of the House Sparrows, in addition to the seven pairs that were usurped by sparrows, another pair breeding in the large-entrance nest boxes was abandoned (we are unsure of the reason why), and one pair breeding in the small-entrance nest boxes was predated.

Behavior in the presence of a competitor

Great Tit pairs in the presence (n = 8 breeding pairs) or absence (n = 9 breeding pairs) of House Sparrows, visited the nest boxes a similar number of times (U = 28.0, P = 0.48), but the former Great Tit pairs spent significantly more time per visit than the latter (U = 8.0, P = 0.006) (Fig. 2). Specifically, in the presence of House Sparrows, the Great Tits spent both more time on the tree of the nest box per visit (U = 15.0, P = 0.033) and more time inside the nest box per visit (U = 15.0, P = 0.043), but only marginally more time in alarm calling (U = 18.0, P = 0.079) (Fig. 2). Aggressive chasing interactions by House Sparrows toward Great Tits were observed during three out of the eight observations (37.5%), including one House Sparrow attacking a Great Tit and pulling out one of its tail feathers upon entering the nest box.

Discussion

In the present study, the influence of House Sparrows on the breeding success and parental care of Great Tits was examined both before and during the House Sparrow breeding season. Great Tit pairs that bred in large-entrance nests, during the period when House Sparrows also bred, fledged significantly fewer young than pairs breeding in the small-entrance nest boxes. This lower reproductive success was a direct result of House Sparrows usurping Great Tit nests in the large-entrance nest boxes, resulting in 77.8% of the Great Tit pairs failing to fledge any young due to the interference competition. As hypothesized, the interference competition was seasonal and only occurred during the period when both House Sparrows and Great Tits were breeding concomitantly.

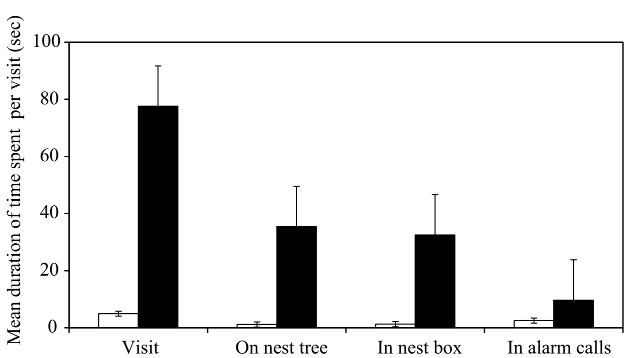

Fig. 2 Comparison between the duration of visit (seconds; mean ± SE) by Great Tit parents on the tree of the nest box, in the nest box, and alarm calls in the presence (n = 8 Great Tit breeding pairs; black) and in the absence of House Sparrows (n = 9 Great Tit breeding pairs; white) during 1-h observation sessions

We found interference competition by House Sparrows usurping nests to be the most limiting factor for the Great Tit breeding pairs. These findings support those of Van Balen et al. (1982), who found that the larger Common Starling (*Sturnus vulgaris*) usurped the smaller Great Tit nests in treatments that gave the larger species access. Even though the worst outcome of nest-site competition, complete nest failure, is similar to that of nest predation (Martin 1993, 1995), there is an ongoing debate as to which is more important for nest selection (Nilsson 1984; Wiens 1992). Nest-site predators and competitors' population densities vary with the potential effect of each probably varying among study sites and areas.

Nest competitors may use active nest cavities as a sign of nest quality, and consequently invest time and risk injury in order to usurp occupied cavities rather than seeking unoccupied cavities (Wiebe 2016). Charter et al. (2013) found that 74% of nest boxes that were occupied by Great Tits at the beginning of the breeding season were later occupied by House Sparrows, even though other empty nest boxes were available. In addition, Gowaty (1981) found that 33% of the nest boxes that were occupied by House Sparrows had been previously occupied by the Eastern Bluebird (*Sialia sialis*). Using nest sites previously occupied by other birds may therefore be similar to a producer-scrounger game, as was found in foraging House Sparrows in which some individuals forage for food while other individuals follow them and exploit the resources found by the former (Katsnelson et al. 2008).

Some species have evolved strategies to avoid interspecific nest-site competition with larger species (Dhondt 2011), such as smaller tit and nuthatch species that excavate their own cavities (Dhondt 2007), while others reduce the entrance size of natural and secondary cavities with mud (Matthysen 1998). Here, Great Tits may alter their ecological niche as a result of nest-site competition with House Sparrows, by changing their preference for specific nest characteristics (e.g., entrance size) and/or the timing of breeding. Earlier breeding by Great Tits might be a strategy to avoid competition (Grether et al. 2009), because Great Tits that breed earlier reduce the risk of interference competition by House Sparrows. In Europe, secondary cavity-nesting passerines that migrate and arrive at breeding sites with larger resident cavity-breeding birds are sometimes unable to breed if nest sites are unavailable (Merilä and Wiggins 1995). In comparison to nest-site competition, selecting small entrances to avoid predation is probably not a major factor in shaping the evolution of cavity-breeding birds in Israel, because the two most common nest predators (Black Rats *Rattus rattus* and Asian Racer *Coluber nummifer*) are able to enter even the smallest entrance nest cavities used for breeding birds.

In environments where birds rely only on old woodpecker holes and/or natural cavities to breed, interference competition may be more intense, especially when such nest cavities are limited. This is relevant in Israel because in addition to House Sparrows, other larger native species such as the Scops Owl (Charter et al. 2010a) and Hoopoe (Charter et al. 2008) also use the same cavities to breed and may further reduce the number of available cavities; while introduction of larger and more aggressive alien species may reduce the number of such sites even more (Pell and Tidemann 1997). For example, the number of nest sites and breeding success of Great Tits were shown to be reduced by two alien invasive species (Common Myna and Rose-ringed Parakeet) (by exploitation competition and interference competition) (Charter et al. 2016). Although the larger species typically usurp the nest sites of smaller species, the opposite can also be true, as found in an experimental study of the larger Mountain Bluebird (*Sialia currucoides*) and the smaller Tree Swallow (*Tachycineta bicolor*) (Wiebe 2016). Certain birds may therefore be more aggressive and different species have different resource-holding potential (Wiebe 2016).

In addition to the Great Tit pairs that failed to fledge young due to interference competition, the Great Tits also behaved differently in the presence of House Sparrows. Specifically, Great Tits increased nest defense by spending more time per visit, both on the tree housing the nest box and inside the nest box. In addition to usurping nest boxes, House Sparrows were also observed attacking Great Tits at the nest boxes. Similar to nest defense against predators, nest defense against nest-site competitors can be just as important because of the risk of nest failure. In locations with many nest-site competitors, parents will need to invest more time in nest defense, which may reduce their ability to bring food, spend time brooding and cleaning the nest, which may ultimately affect breeding success. They may therefor face a trade-off between these activities, especially when activity time is limited (Brown 1988). Such trade-offs may be more severe during the breeding season, in which energy expenditure peaks: for example birds such as the Orange-tufted Sunbird (*Nectarinia osea*) demonstrate a trade-off between feeding their young and spending time mobbing potential predators (Markman et al. 1995).

In conclusion, both exploitation and interference competition may act alone or together, directly or indirectly, to impact parental behavior and reproductive success. In this study we were able to demonstrate that both parental behavior and reproductive success of the Great Tit were negatively affected by their larger House Sparrow competitor. However, there remains an urgent need for additional experimental studies focused on competition between two species for one only resource (rather than on species that compete for both nest sites and food) in order to determine to what extent the presence of nest-site competitors and predation risk versus interference competition may affect parental care and breeding success.

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