

## Extra-pair copulation and paternity defense in the hihi (or stitchbird) *Notiomystis cincta*

John G. Ewen<sup>1\*</sup>, Doug P. Armstrong<sup>1</sup>, Brice Ebert<sup>1</sup> and Lars H. Hansen<sup>2</sup>

<sup>1</sup>Wildlife Ecology Group, Institute of Natural Resources, Massey University, Palmerston North, New Zealand

<sup>2</sup>Behaviour Group, Department of Population Biology, Zoological Institute, University of Copenhagen, Copenhagen, Denmark

\*Address for correspondence: Laboratoire de Parasitologie Evolutive, CNRS UMR 7103, Université Pierre et Marie Curie, 75252 Paris Cedex 05, France (E-mail: john.ewen@snv.jussieu.fr)

**Abstract:** Extra-pair copulation (EPC) occurs frequently in hihi (stitchbird), *Notiomystis cincta*, resulting in a high rate of extra-pair paternity. It occurs despite resistance by females, and is often witnessed by the paired male. We studied male behaviour to assess whether extra-pair males were timing copulation attempts to coincide with peaks in female fertility, and whether paired males were behaving in ways to reduce cuckoldry. Extra-pair males concentrated copulation attempts at peaks in female fertility. Paired males attempted to defend their paternity by defending an area around the nest site, by territorial calling and displacing intruding males. The frequency of EPC attempts varied between nests and this variation mirrored closely the variation in the percentage of extra-pair paternity. Potential additional paternity guards, such as frequent copulation, did not occur in this population.

**Keywords:** mating system; extra-pair copulation; hihi; stitchbird; paternity defense.

### Introduction

Extra-pair copulation (EPC) occurs in many bird species and has been shown to result in extra-pair paternity (Birkhead and Møller, 1995). An EPC occurs when a male mates with a female paired with another male (Parker, 1990). Trivers (1972) suggested that a male's reproductive success is limited by his access to females rather than his rate of sperm production. Males may overcome this restriction by gaining extra-pair copulations. In birds, a large time window exists for males to successfully fertilise eggs of a given female. This is because females of most bird species can store viable sperm in specialised sperm storage tubules (Birkhead *et al.*, 1991; Birkhead and Hunter, 1990). Although sperm storage varies from 6–45 days among bird species (Birkhead and Moller, 1993), female fertility peaks 2–3 days before egg laying (Westneat, 1987; Colgrave *et al.*, 1995).

The success of EPCs in achieving fertilisation will depend on: 1) the timing of copulation relative to the female's fertile period (Colegrave *et al.*, 1995; Birkhead *et al.*, 1987); 2) the relative amounts of sperm ejaculated by males (Birkhead, 1995; Gomendio and Roldan, 1993); and 3) potential post-copulatory control by the female (Birkhead *et al.*, 1993). While EPC increases the reproductive success of some males, it generally

decreases the reproductive success of the paired male. In most cases it is accepted that paired males will maximize reproductive success by preventing EPCs from occurring (but see Jamieson *et al.*, 1994). Competition for paternity has resulted in a range of elaborate paternity defense behaviours including mate guarding, guarding resources necessary for reproduction and frequent copulation (Briskie, 1992; Birkhead, 1995; Beasley, 1996; Macdougall-Shackleton *et al.*, 1996).

In this study we investigated the reproductive behaviour of a small, isolated and reintroduced population of hihi (stitchbirds), *Notiomystis cincta*. Extra-pair copulation has been observed previously in another population of this species (Castro *et al.*, 1996), and high levels of extra-pair paternity have been documented in the current study population (Ewen *et al.*, 1999). Reproductive anatomy of this species is typical of a species with high levels of competition for reproductive success (including large testes, 4.2% of body mass), large cloacal protuberances, large seminal glomera and large numbers of sperm in the seminal glomera; Castro *et al.*, 1996). Mating behaviour of hihi also indicates intense competition for mating opportunities. Resisted face-to-face copulations (unique to this species) are commonly observed in this and other populations (Ewen *et al.*, 1999; Castro *et al.*,

1996) and these behaviours have also been directed toward non-reproductive fledgling birds (see Ewen and Armstrong, 2002 for discussion).

We aimed to determine whether: (1) paired males attempted to defend their paternity by mate guarding or guarding resources necessary for females to successfully breed, (2) extra-pair males timed their EPCs to coincide with peaks in female fertility, and (3) patterns of observed EPC attempts correlated with levels of extra-pair paternity.

## Methods

### Study site and population

Hihi are an endangered, medium-sized forest passerine endemic to New Zealand. They are sexually dimorphic, with the males weighing on average 30% more than females (Armstrong and Ewen, 2001). The male has a black head, golden shoulders and breast band, white erectile 'ear' tufts and a white wing bar (Rasch *et al.*, 1996). In comparison, the relatively dull female is predominantly olive brown, while also having a distinctive white wing bar (Craig, 1985). Hihi are cavity nesters and will nest in nestboxes (Rasch, 1989). Females usually lay 4–5 eggs per clutch and may have up to three clutches from October to February (Rasch, 1985; Armstrong *et al.*, 1997). Females do all nest building and incubation but the paired male does contribute to provisioning (Ewen and Armstrong, 2000). Hihi are usually socially monogamous, but they can also be polygynous and polygynandrous (Castro *et al.*, 1996).

Hihi were translocated to Tiritiri Matangi Island in 1995 (with additional birds released in 1996) as part of a conservation initiative aimed at increasing the species' range and numbers (Rasch *et al.*, 1996). Tiritiri Matangi Island is 3 km off Whangaparaoa Peninsula, 25 km north of Auckland, New Zealand. The 220 ha island has a gentle topography with broad ridges sloping away from the main longitudinal ridge (60–80 m altitude). Forest remnants cover about 50% of the island, mostly as young coastal forest (Wilson, 1997). Due to the lack of mature forest trees with natural cavities, hihi nested in artificial nesting boxes provided in all forest patches on the island.

The breeding behaviour of hihi was observed over their first two breeding seasons on the island (1995/96 and 1996/97). In both years the adult sex ratio was heavily skewed toward males, 12:4 in 1995/96 and 12:6 in 1996/97, largely as a result of differential survivorship of the sexes immediately after translocation. Nine nesting attempts were observed. All individuals were banded with unique combinations of wrap-around C-size plastic bands and a numbered aluminum band.

### Sampling regime

Observations of breeding behaviour were initiated as early in the reproductive cycle as possible (range 15 to 3 days before egg laying and indicated by commencement of nest building). Systematic searches of hihi nest boxes and general observation of behaviour usually enabled early identification of nesting.

Flagging tape was used to mark a circular area of 30 m radius around each nest site. Observations were restricted to within this area allowing direct comparisons between nests. This distance was chosen based on earlier observations of hihi breeding on Kapiti Island by Castro *et al.* (1996) who found that paired males would call and behave aggressively toward other males within a 30 m radius of their nesting tree. The observer would move quietly around the 30 m perimeter. These movements were largely restricted to the boardwalks and tracks provided for the large numbers of people viewing birds and vegetation on the island (an open sanctuary).

Behavioural observations were conducted at three time intervals each day, from when the nest site was discovered to when egg laying was complete. The three time intervals, two hours in duration, were 06:30–08:30, 11:00–13:00 and 16:00–18:00. The observation time was divided equally among nests. Due to nesting asynchrony there were never more than two nests to observe at one time. Therefore, each nest was usually observed for at least 50 min per time period, allowing time to move between nest sites within each set time interval.

An all-occurrence sampling regime (Martin and Bateson, 1993) was used to record hihi breeding behaviour. We recorded all copulation attempts, territorial calls by the paired male, and displacements of intruding extra-pair males by the paired male. Additionally, we recorded the amount of time the paired male and female spent within the 30 m radius of the nest and all sightings of extra-pair males and females. A measure of each extra-pair male's presence was obtained by tallying all instances when they were involved in defined behaviours, i.e. we counted every time an individual was seen being displaced, attempting to copulate, calling, visiting the nest box, or seen while we searched the area within 30 m radius of the nest, regardless of whether it had left the area or not in the intervening period. Those individuals counted more times within the nesting area were assumed to spend more time there. Data were recorded with a microcassette recorder, and later transcribed.

For most copulation attempts, we recorded whether or not copulation occurred. As this was not always possible, e.g. when the female was chased from the nesting area, the data may underestimate the number of copulations. Copulation was considered to occur if a male mounted the female's back and cloacal contact

was achieved or if he mounted the female in the face-to-face position described by Castro *et al.* (1996). Copulations were divided into (a) those apparently resisted by the female, and (b) those apparently solicited by either a male or female. Some extra-pair copulation attempts occurred while the female was inside the nest box. This was deduced by observing an extra-pair male entering a nest box with a female already inside and the subsequent sounds emitted. These sounds (female distress calls, and noisy movement of wings or bodies) were similar to sounds heard during face-to-face copulations observed outside the nest box (see below). Further, a single nest built in an alternative nest box design (with a mesh front) allowed observation of these copulation attempts. Again similar sounds were heard and successful copulation (in a face-to-face position) was achieved. We also, therefore, assumed copulations in the nest box were successful given the limited ability of the female to resist and escape an extra-pair male.

### Data analysis

The proportion of time the paired male and female spent within 30m of the nest was calculated per hour of observation. Because one or both birds in a pair were often absent from the sample area, frequencies of some behaviours were recorded for the time the individual was in sight. The frequency of copulations and attempted copulations were calculated per female per hour. Displacements of extra-pair males by paired males were calculated per paired male per hour. Any frequencies calculated from individuals spending less than 10% of their time in the territory were excluded from the analysis to avoid large inflation in frequencies (calculated per hour).

Paired *t*-tests were used to test: (1) whether paired males and females differed in the proportion of time spent on their territories, and (2) whether territorial call rates of paired males were different when the female was present than when she was absent.

Regression analysis was used to investigate the relationship between: (1) within-pair copulation attempts and EPC attempts, and (2) frequency of EPC attempts and % paternity within each nest. An average rate was calculated for each nest over the period from 7 days before egg laying until clutch completion (the approximate fertile period of the female). Each nest was observed for an equal number of hours at each of five different stages: 5–7 days before laying, 3–4 days before laying, 1–2 days before laying, 1<sup>st</sup>–2<sup>nd</sup> day of laying, and 3<sup>rd</sup>–5<sup>th</sup> day of laying. Therefore, differences among nests are not biased by changes in EPC over the reproductive cycle.

Mixed model ANOVA with a Poisson error term was used to test whether presence of extra-pair males, attempted extra-pair copulations, difference in call

rate, total call rate and frequency of displacements by paired males varied according to stage of breeding, for the five stages listed above. Differences between individual females were controlled by including female as a random factor in all models. The individual observation sessions were treated as the unit of replication. This was necessary to test for changes over time, given the small size of the population. This means that the results apply only to the individuals studied, but this is appropriate since these individuals make up the entire population.

Data on call rates and percentage-shared paternity were log transformed and percentages of time males and females spent near the nest were arcsine transformed in order to normalise the respective data sets. Means are expressed  $\pm$  SE unless otherwise stated.

## Results

### Extra-pair male behaviour

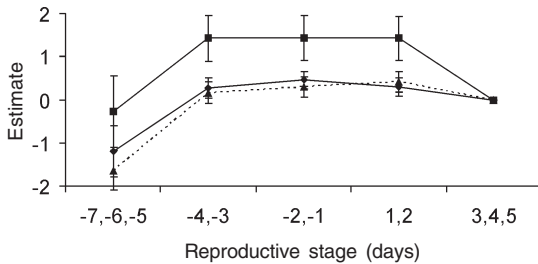
In total, 333 attempted EPCs were observed, of which 36 resulted in copulation. All these EPCs were “face-to-face” copulations and/or copulations in the nest box (where birds could not be observed), and all appeared to be resisted by the female. Resistance took the form of trying to fly away from the male or males, and repeated alarm calls.

Extra-pair males entered the nesting area of fertile females (Fig. 1) both when the females were present and when they were absent. These extra-pair males included both unpaired males and paired males whose mates were not in their fertile period. Presence of extra-pair males increased significantly as females approached egg laying, then decreased toward the end of egg laying ( $F_{4,177} = 2.84$ ,  $P < 0.026$ ) (Fig. 1).

Extra-pair copulations were attempted throughout some females' fertile periods. Observation of two females who were sampled from 15 days before egg laying showed extra-pair males attempted to copulate at least 12 days before egg laying. The first extra-pair copulation was also observed 12 days before egg laying. The timing of EPC attempts followed the pattern observed for extra-pair male presence, being highest during the female's fertile period ( $F_{4,176} = 3.39$ ,  $P = 0.011$ ) (Fig. 1). Copulation attempts continued throughout egg laying and some copulations occurred after egg laying was completed.

### Attempted-EPC frequency and actual paternity

Levels of extra-pair paternity varied among nests, with the percentage of young resulting from EPC ranging from 0 to 75% (Ewen *et al.*, 1999). Nests with the highest rate of EPC attempts had a lower percentage of young fathered by paired males ( $F_{1,7} = 17.641$ ,  $P = 0.004$ ) (Fig. 2).



**Figure 1.** Estimates ( $\pm$  SE) based on the standardised Normal and generated from mixed model ANOVAs investigating changes across five reproductive stages (denoted by days relative to egg laying) in (a) extra pair male presence, denoted by solid line and diamonds, (b) frequency of extra-pair male displacements by the paired male, denoted by dashed line and triangles and (c) attempted EPC rates, denoted by solid line and squares. All estimates are calculated relative to the fifth reproductive stage. Female was included in all models as a random factor.

### Paternal defense by paired males

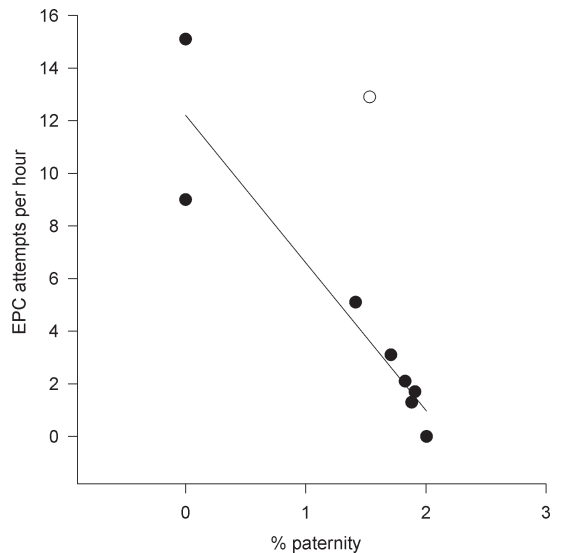
Hihi always formed socially monogamous pairs despite the heavy bias toward males in this population and evidence of polyandry in the Kapiti Island population (Castro *et al.*, 1996). Paired male hihi spent significantly more time within 30 m of the nest box than the female (paired sample *t*-test,  $t_8 = 14.305$ ,  $P < 0.001$ ). Males were present 77% of the time, and females for 33% of the time on average, and both male and female presence remained consistent throughout the recorded period (Fig.3). It was also consistent up to 15 days before egg laying for the two pairs observed that long. Males were near the nest site 61% of time when the female was present and 67% when she was absent. This suggests males spent more time guarding nests than guarding females, i.e. when females were away from nests, males spent 67% of their time near the nest, leaving a maximum of 33% of time they could be guarding the female. In addition, when females were near the nest males were often not present indicating further that female presence does not completely govern male presence at the nest.

Paired males gave territorial calls both when the female was present and absent. However, call rates were significantly higher when the female was present (paired sample *t*-test;  $t_8 = 5.256$ ,  $P < 0.001$ ), rising from a mean of 1.35 calls per minute to 3.34 calls per minute. This difference in call rate remained consistent throughout the measured fertile period ( $F_{4,107} = 0.23$ ,  $P = 0.92$ ) and males did not significantly change their overall call rate with respect to the females' fertile period ( $F_{4,165} = 0.95$ ,  $P = 0.437$ ).

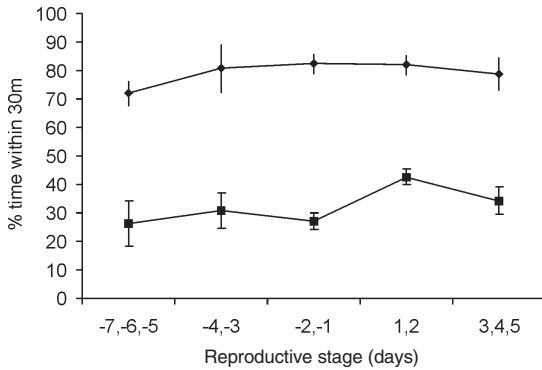
Male hihi also defended their nest areas by attempting to displace extra-pair male intruders both

when the female was present and absent (Fig.1). The rate of displacements increased as females progressed through their fertile periods, peaking during egg laying ( $F_{4,141} = 5.63$ ,  $P < 0.001$ ). This trend was similar to that measured for extra-pair male presence ( $F_{4,177} = 2.84$ ,  $P = 0.026$ ).

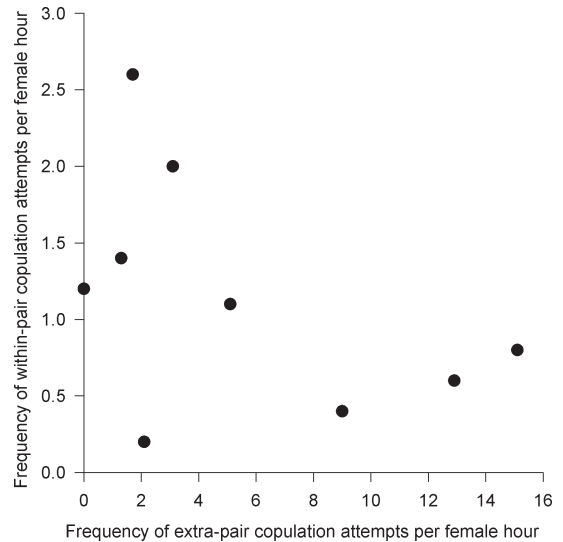
In contrast to EPC, the majority of observed within-pair copulations were solicited by either the male or female in a non-forceful manner (60% of the 22 observed copulations). Data from the two females sampled for extended periods showed that attempted within-pair copulations occurred up to 15 days before the first egg was laid and successful copulation occurred up to 11 days before egg laying. It is interesting to note that forced within-pair copulations did occur, and that many solicitation events by both members of a pair were frequently ignored by their mate (19% of a females solicitations and 34% of a males). Despite the presence of forced within-pair copulation, there was no significant relationship between the frequency of within-pair copulation attempts at a nest and the frequency of EPC attempts ( $F_{1,1} = 1.918$ ;  $P = 0.209$ ). This result occurred even though there was great variation in both within-pair and extra-pair copulations (Fig.4).



**Figure 2.** Paired males' percentage share of paternity (log transformed) within broods in relation to attempted EPC rates over the fertile period of the female. Each point represents an individual nest. The line was fitted using simple linear regression through all points except the identified outlier (indicated as an open circle).



**Figure 3.** Time spent within 30 m of the nest site by the paired male (circles) and the female (squares) in relation to egg laying (expressed as days included within each of the five reproductive stages). Values are means  $\pm$  SE, using nests as the units of replication.



**Figure 4.** Relationship between the frequency of extra-pair copulation attempts and within-pair copulation attempts. Each point represents an individual nest.

## Discussion

Our results support the hypothesis that paired male hihi guard nest sites rather than guarding females directly. Males spent significantly more time within 30 m of the nest site than females. Males gave territorial calls and attempted to displace extra-pair males, regardless of female presence. Territory defense in hihi is restricted to the breeding season and is centered on the nest site, lasting only as long as such sites are active. In addition, only active nest boxes (i.e. those associated with a female) were defended, with additional defended areas sometimes established by males other than the social mate in close proximity to the active nest site (J.Ewen *pers. obs.*). Such territoriality, especially centered on the period when a male's partner is fertile, is seen in many bird species and regarded as a form of paternity defense (Birkhead, 1995). Female hihi on average spent only 33% of their time within 30 m of the nest, suggesting nest defense may be a poor form of paternity assurance. Males may be facing some form of trade-off between defending the nest site and guarding their mate (Lifjeld and Marstein, 1994), both of which are viewed as best-of-a-bad-job strategies (Birkhead and Møller, 1992; Møller and Birkhead, 1993; Lifjeld and Marstein, 1994). This often occurs in colonial species where feeding sites are distant from the breeding colony (e.g., common murre *Uria aalge*; Birkhead *et al.*, 1985; montezuma oropendolas *Pasarocolius montezuma*; Webster, 1995) and is thought to result in increased opportunities for EPC (Westneat *et al.*, 1990).

From the extra-pair male's perspective, mate guarding restricted to nesting sites creates a potential

for EPCs with the female when she is away from the nest (Birkhead *et al.*, 1987). Females may take advantage of this by actively soliciting copulations (e.g. eastern bluebirds *Sialia sialis*; Gowaty and Bridges, 1991) or may be subject to forced copulations while not protected by her mate (e.g. white-fronted bee-eater *Merops bullockoides*; Emlen and Wrege, 1986). Given that female hihi spent such large amounts of time away from the nest site there was potential for extra-pair copulation (either solicited or resisted). We were unable to assess this because our observations were restricted to the nest site. It would certainly be a worthwhile focus of future research.

However, despite the large amount of time females were away from their nest sites, and the high level of nest site guarding from her mate, extra-pair males continued to attempt copulating with females near the nest. Attempted EPCs near nest sites also occur in colonial species, where one cost of social living is the increased social harassment by conspecifics (Alexander, 1974). Emlen and Wrege (1986) suggested that breeding female white-fronted bee-eaters, *Merops bullockoides*, constitute a reliable resource, i.e. they are predictable both in space and time. Males take advantage of this by chasing females and attempting forced copulations at the colony. Although hihi are not colonial breeders, the data suggest a similar result in that extra-pair males could successfully encounter females at nesting sites and all observed copulation attempts were forced.

Extra-pair male presence near the nest increased significantly as females progressed through their fertile periods. Their presence peaked around one to two days before egg laying and started to decline after egg laying commenced. A similar peak was observed for extra-pair copulation attempts. Such behaviours suggest that extra-pair males had some knowledge of the females' fertile periods and were timing their presence and copulations to coincide. The egg is fertilised soon after ovulation, which in birds occurs soon after the previous egg is laid (Drachmann *et al.* 1997). Although copulations occurring during this period (insemination window) can potentially result in fertilisation (Cheng *et al.*, 1983), insemination is thought to be less effective close to egg laying because sperm retention is low at this time (Birkhead *et al.*, 1996). A peak in female fertility has been reported to occur two to three days before the onset of egg laying (Westneat, 1987 and references therein; Colegrave *et al.*, 1995). Timing of extra-pair copulation attempts in hihi was similar to this, and copulations made during this time probably coincided with peaks in female fertility.

Paired males attempted to prevent other males from forcibly copulating with their partners. Such forced copulations were sometimes successful despite the efforts of paired males (Ewen *et al.*, 1999). Knowledge of EPCs may affect a paired male's certainty of paternity and is predicted to result in additional paternity guards (see examples in Parker, 1990). Knowledge of EPCs has been shown to cause a reduction in provisioning investment in the young (Ewen and Armstrong, 2000). A paired male's investment in mate guarding is costly (Komdeur, 2001) and as noted earlier has been described as a best-of-a-bad-job strategy, especially where females control EPCs (Birkhead and Møller, 1992; Møller and Birkhead, 1993; Lifjeld and Marstein, 1994). Similar conclusions can be drawn with hihi, where forced EPC occurs despite paired males' guarding efforts and these copulations likely result in extra-pair paternity (Ewen *et al.*, 1999). Despite paired males witnessing EPCs with their mates, there appears to be no additional paternity guard behaviours such as frequent copulation (Birkhead *et al.*, 1987; Møller and Birkhead, 1991) although, interestingly, forced within-pair copulations did occur. The reasons why males may ignore female solicitations and also perform forced copulation at different times warrants further and more refined investigation. Males might focus their copulation attempts to follow successful EPC (consistent with copulation as a form of paternity defense, see references above), but we are unable to assess this.

The frequency of attempted EPCs was strongly correlated with the actual paternity within each hihi nest. These results are similar to those found in indigo

buntings (Westneat, 1988). Studies of alpine accentors (Hartley *et al.*, 1995) and polyandrous dunnocks (Burke *et al.*, 1989; Davies *et al.*, 1992) have also revealed reliable behavioural indicators of actual paternity. However, observations of copulations do not always give a good measure of paternity. In many species, DNA fingerprinting has revealed the presence of extra-pair paternity even though behavioural observation concluded EPC to be very rare (e.g. indigo buntings, Westneat, 1990; red-winged blackbirds, Gibbs *et al.*, 1990; Westneat, 1992, 1993; tree swallows, Lifjeld *et al.*, 1993). The close relationship between EPC and paternity that we observed may exist because all extra-pair copulations were forced, and generally quite conspicuous. This close relationship suggests that field observations accurately estimated copulation frequencies. Additionally, as all observed attempted EPCs were resisted by the female, it indicates that resisted copulations may result in paternity. It is possible, however, that females which suffer high rates of resisted EPC may also seek EPCs away from the nest (if poor mate guarding indicates social mates are of low quality). Whether resistance by females is to prevent EPCs, or is a more subtle form of quality assessment [Eberhard (1996) proposed females may resist to test male quality] is unknown. For these reasons, a close examination of how females may control these situations and select males as preferred copulation partners would be interesting.

Our study provides the first detailed quantification of mating behaviour in hihi — a species characterised by its intense competition for mating opportunities. The results certainly substantiate this competition and provide a template for further investigations into the mating behaviour of this species. Given the numerous costly reproductive behaviours detailed in this population, future investigation may also be fruitful in terms of understanding the limited population viability in this endangered species.

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