



Flexibility but no coordination of visits in provisioning rifleman



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Parental care strategies occupy a continuum from fixed investments that are consistent across contexts to flexible behaviour that largely depends on external social and environmental cues. Determining the flexibility of care behaviour is important, as it influences the outcome of investment games between multiple individuals caring for the same brood. We investigated the repeatability of provisioning behaviour and the potential for turn taking among breeders and helpers in a cooperatively breeding bird, the rifleman, *Acanthisitta chloris*. First, we examined whether nest visit rate is an accurate measure of investment by assessing whether carers consistently bring the same size of food, and whether food size is related to nest visit rate. Our results support the use of visit rate as a valid indicator of parental investment. Next, we calculated the repeatability of visit rate and food size to determine whether these behaviours are fixed individual traits or flexible responses to particular contexts. We found that rifleman were flexible in visit rate, supporting responsive models of care over 'sealed bids'. Finally, we used runs tests to assess whether individual rifleman alternated visits with other carers, indicative of turn taking. We found little evidence of any such coordination of parental provisioning. We conclude that individual flexibility in parental care appears to arise through factors such as breeding status and brood demand, rather than as a real-time response to social partners.

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Parental investment is a critical component of most animal life histories, and understanding variation in parental investment is key to research in behavioural adaptation and life history trade-offs, because of the importance of reproduction in determining individuals' inclusive fitness. Levels of investment observed in natural populations are expected to be products of coevolution between carers and dependent offspring (Hatchwell, 1999; Hinde, Kilner, & Johnstone, 2010; Trivers, 1972, 1974). In addition, individuals are expected to adjust their contributions to care in relation to the social and environmental context, if doing so can increase their reproductive success.

Theoretical work has explored a range of different assumptions about behavioural flexibility during parental care. Houston and Davies (1985) modelled parental investment as a fixed, per-individual 'sealed bid', optimized over evolutionary time. From this theoretical framework, we would expect clear individual

consistency in parental investment, persisting across multiple observations. Studies of house sparrows, *Passer domesticus*, have supported this prediction, especially in males (Nakagawa, Gillespie, Hatchwell, & Burke, 2007; Schwagmeyer, Mock, & Parker, 2002). In contrast, more recent models incorporate behavioural plasticity through 'negotiation', in which individual parents vary their investment depending on the behaviour of their partner (Johnstone, 2011; McNamara, Gasson, & Houston, 1999). Johnstone et al. (2014) have shown that 'conditional cooperation', in which carers visit following their partners' visits, is a stable negotiation mechanism that maximizes benefits to offspring. This response rule implies that carers should take turns visiting offspring, a prediction borne out in studies of provisioning great tits, *Parus major* (Johnstone et al., 2014), chestnut-crowned babbler, *Pomatostomus ruficeps* (Savage, 2014), long-tailed tits, *Aegithalos caudatus* (Bebbington & Hatchwell, 2016) and acorn woodpeckers, *Melanerpes formicivorus* (Koenig & Walters, 2016). The empirical support for both sealed bid and negotiation-based models suggests that both can provide evolutionary solutions to the organization of parental care, with systems occupying different points along a continuum between

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complete inflexibility (sealed bids) and extremely responsive negotiation (Hinde & Kilner, 2007).

Plasticity in an individual's investment can also arise from factors other than their partner's behaviour. These may relate to an individual's own condition, characteristics of its partner or helpers, or extrinsic cues such as offspring demand, food availability or predation pressure (Brouwer, Van de Pol, & Cockburn, 2014; Ghaleb, Peluc, & Martin, 2013; Naef-Daenzer & Keller, 1999). Such factors can generate noise when attempting to measure between-individual differences in behaviour. In cooperative breeders, species with nonparent contributors to care, behavioural flexibility may also take the form of 'load lightening', wherein a parent's investment depends on the extent of provisioning by helpers (Crick, 1992; Hatchwell, 1999). Observed plasticity in parental care may therefore be a product of a number of factors, including social negotiation.

Robust measures of investment are required to investigate the coevolutionary processes underlying parental care strategies (Browning et al., 2012). In birds, parental investment is commonly measured by counting provisioning visits made by carers to dependent offspring over a certain period. This 'visit rate' is used to quantify a parent's contribution to care, relative to the investment of its partner, helpers or other parents in the population (e.g. Davies, 1986; Kilner, Madden, & Hauber, 2004; Nam, Simeoni, Sharp, & Hatchwell, 2010). Visit rate is also useful for comparing the same individual across time, within or between breeding attempts. Despite the convenience of using visit rates as an index of investment, the value of food items that carers bring can also be important. For example, although consideration of food size has shown visit rate alone to be a robust measure of food delivery in house finches, *Carpodacus mexicanus* (Nolan, Stoehr, Hill, & McGraw, 2001) and chestnut-crowned babbblers (Browning et al., 2012), higher visit rates in house sparrows (Schwagmeyer & Mock, 2008) and house wrens, *Troglodytes aedon* (Bowers, Nietz, Thompson, & Sakaluk, 2014) correspond with parents bringing smaller food items, meaning that visit rate is largely unrelated to contributions to care. Visit rate alone is also a less meaningful measure if individual carers are consistent in the sizes of food they bring to offspring (e.g. individuals bringing relatively large food items have their contribution underestimated by visit rate). We might expect to observe these patterns because of between-individual differences in quality or foraging strategies (Bell, Hankinson, & Laskowski, 2009; Dall, Houston, & McNamara, 2004; Smith & Blumstein, 2008). Food size is, therefore, a potentially important consideration when measuring investment during provisioning, but the effects of the social environment on both visit rate and load size have rarely been investigated in cooperative breeders.

We studied investment in offspring through observations of nestling provisioning by parents and helpers in rifleman, *Acanthisitta chloris*. Rifleman are small (5–7 g) insectivorous passerines endemic to New Zealand. Pairs may breed up to twice in a season, laying two to five eggs in each breeding attempt. Chicks hatch on the same day and remain in the nest for about 24 days before fledging (Withers, 2013). Brood sex ratios are apparently random with no evidence of departure from parity (Sherley, 1993). Rifleman are facultative cooperative breeders, with two to six individuals provisioning at nests observed in our study. Rifleman helpers are unusually variable, as they may be adult or juvenile, paired or unpaired, successful or unsuccessful breeders, and they do not necessarily share a territory with the breeders that they help; however, they are almost always close relatives of the nestlings they provision (Preston, Briskie, Burke, & Hatchwell, 2013; Sherley, 1990). Nestlings attended by adult helpers receive more provisioning visits, and enjoy better survival prospects, than those in

nests without helpers (Preston, Briskie, & Hatchwell, 2016). Breeders are known to provision more than helpers, and male breeders more than females (Preston et al., 2013), but finer-scale variation in individual provisioning has not yet been investigated. In this study, we tested whether a sealed bid or negotiation-based model of investment better explained variation in provisioning by rifleman. To test each model, we first needed to establish that visit rate was a reliable measure of investment, by assessing whether individual carers consistently brought the same size of food items and whether food size was related to nest visit rate. We then investigated whether investment is repeatable, as envisaged by the sealed bid model, or flexible within individuals. Finally, we considered whether the observed variation in caring behaviour is a response to the investment of other carers, or simply dependent on factors such as brood demand.

METHODS

Data Collection

We studied a small (6–11 pairs) nestbox population of rifleman at Kowhai Bush (173°37'E, 42°23'S), near Kaikoura on New Zealand's South Island, between September and January from 2012 to 2015. Kowhai Bush is a temperate seral forest dominated by kākūka, *Kunzea ericoides*; the mean annual temperature is 12 °C, and the mean annual rainfall 865 mm (Gill, 1980). Most pairs attempted to breed twice during a season, even when their first brood was successful. In total, provisioning data from 46 different individuals at 33 nests were used for this study; 15 (45%) of these nests were attended by parents and one to four helpers, with the remainder attended by parents only.

Active nests were identified before eggs hatched by weekly checking of all nestboxes on the study site for the presence of nests, and daily checks of those containing nests. Each individual in the population was given a unique combination of two colour rings and a metal Department of Conservation AP ring for identification, either as a 15-day-old nestling, or as an adult or juvenile caught by mist netting near to known nests.

Each nest was filmed using a digital camcorder every 3 days after hatching when possible, starting at day 3, where hatching is defined as day 0, and continuing until fledging. Nestlings typically fledged around day 24. Each recording started with a 15 min acclimatization period for which footage was discarded, with data then collected from the following hour. Recording start time varied between 0700 and 1700 NZST. Carers were not caught on the days their nests were filmed.

After nests were filmed on day 15, each nestling was temporarily removed from the nest to be weighed, measured, ringed, sexed, and have samples taken of blood (15 µl from the brachial vein for genetic analysis) and preen wax (for chemical analysis). Rifleman are sexually dimorphic and can be sexed reliably in the hand at day 15, females being larger than males (mean female mass = 8.48 ± 0.10 g SE; mean male mass = 7.49 ± 0.06 g SE) with differently coloured plumage. At least one nestling was always left in each nest so that adults did not return to an empty nest, which may stimulate abandonment.

Videos were all transcribed by a single observer. For each visit in a video, the start and end time (accurate to 1 s), individual identity (recognized using colour-ring combination), sex, type of behaviour (brooding, successful/unsuccessful feeding, bringing/removing feathers, removing faecal sacs or unknown) and size of food brought for feeding visits were all noted. Food size was estimated relative to bill size (small = smaller than one-third of bill size, medium = between one-third and full bill size, large = larger than full bill size). Rifleman do not regurgitate food, and all food

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