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Parental care strategies occupy a continuum from fixed investments to flexible behaviour that depends on external cues. Such variation in care strategies 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 species, the rifleman *Acanthisitta chloris*. First we examined whether nest visit rate is a meaningful 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 load size to determine whether these behaviours are fixed individual traits or flexible responses to particular contexts. We found that riflemen were highly flexible in visit rate, supporting responsive models of care over 'sealed bids'. Finally, we used runs tests to assess whether individual riflemen alternated visits with other carers, symptomatic 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.

Keywords *Acanthisitta chloris*; cooperative breeding; negotiation; parental care; repeatability; rifleman

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 parents, additional carers (in cooperative breeders), and dependent offspring (Trivers, 1972, 1974; Hatchwell, 1999; Hinde et al., 2010).

Houston and Davies (1985) modelled parental investment as a fixed, per-individual 'sealed bid', optimised over evolutionary time. From this theoretical framework we would expect clear individual consistency in parental investment, persisting across multiple observations. Studies of house sparrows have supported this prediction, especially in males (Schwagmeyer et al., 2002; Nakagawa et al., 2007). In contrast, more recent models incorporate behavioural plasticity through 'negotiation', in which individual parents vary their investment depending on the behaviour of their partner (McNamara et al., 1999; Johnstone, 2011). Johnstone et al. (2014) have shown that 'conditional cooperation', in which carers are more likely to visit following their partners' visits, is a stable negotiation mechanism that maximises 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 babblers *Pomatostomus ruficeps* (Savage, 2014) and long-tailed tits *Aegithalos caudatus* (Bebbington and Hatchwell, 2016). The empirical support for both sealed bid and negotiation-based models suggests that both can provide evolutionary solutions to the organisation of parental care. Hinde and Kilner

(2007) have proposed that systems occupy different points along a continuum between complete inflexibility (sealed bids) and extremely responsive negotiation.

Plasticity in individuals’ investment can also arise from factors other than their partners’ behaviour. These may relate to an individual’s own condition, characteristics of their partner or helpers, or extrinsic cues such as offspring demand, food availability, or predation pressure (Naef-Daenzer and Keller, 1999; Ghalambor et al., 2013; Brouwer et al., 2014). Such factors can generate noise when attempting to measure between-individual differences in behaviour. In cooperative breeders, behavioural flexibility may also take the form of ‘load-lightening’, where 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 either social negotiation, other factors, or a combination.

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 the number of 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 (Davies, 1986; Kilner et al., 2004; Nam et al., 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 et al., 2001) and chestnut-crowned babblers (Browning et al., 2012), higher visit rates in house sparrows *Passer domesticus* (Schwagmeyer and Mock, 2008) and house wrens *Troglodytes aedon* (Bowers et al., 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 this because of between-individual differences in quality or foraging strategies (Dall et al., 2004; Smith and Blumstein, 2008; Bell et al., 2009). 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 alloparents in riflemen *Acanthisitta chloris*. Riflemen are small (5-7 g) insectivorous passerines endemic to New Zealand. Pairs may breed up to twice in a season, laying 2-5 eggs in each breeding attempt. Chicks hatch on the same day and remain in the nest for c.24 days before fledging (Withers, 2013). Brood sex ratios are apparently random with no evidence of departure from parity (N. Khwaja and S. A. J. Preston, unpublished). Riflemen are facultative cooperative breeders, with 2-6 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 (Sherley, 1990; Preston et al., 2013). Nestlings attended by adult helpers receive more provisioning visits, and enjoy better survival prospects, than those in unhelped nests (Preston et al., 2016). Breeders are known to provision more than helpers, and male breeders more than females (Preston et al., 2013). More fine-scale variation in individual provisioning has not yet been investigated. In this study, we aimed to test which models of the evolution of investment were applicable in riflemen. In order to do so, we first needed to establish a reliable measure of investment, and so we critically examined whether visit rate was appropriate. We then investigated whether investment is repeatable, as envisaged by the sealed bid model, or is 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 riflemen at Kowhai Bush (173° 37’ E, 42° 23’ S), near Kaikoura on New Zealand’s South Island, between September and January from 2012-2015. Kowhai Bush is a temperate seral forest dominated by kanuka (*Kunzea ericoides*); mean annual temperature is 12 C, and 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 1-4 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-minute acclimatisation 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 (for genetic analysis) and preen wax (for chemical analysis). Riflemen 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 SE; mean male mass = 7.49 ± 0.06 SE) with differently coloured plumage. At least one nestling was left in each nest at all times 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 one second), individual identity (recognised 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). Riflemen do not regurgitate food, and all food delivered to the nest is held in the bill. Nestlings are provisioned with small invertebrates, chiefly adult and larval moths, spiders, crickets and weta (Preston et al., 2013). For the purpose of the analyses presented here, non-feeding visits were removed from the data. All statistical analyses were implemented in R 3.2.2 (R Development Core Team, Vienna).

Testing the Relationship Between Visit Rate and Load Size

We examined the relationship between load size and visit rate using a Spearman's rank correlation test, by comparing the number of large and non-large (sum of medium and small) food items brought by each individual for each recorded hour. If carers visiting infrequently compensate by bringing larger food, we would expect a negative relationship between these two variables. We chose non-large food items rather than total number of visits because the latter is automatically correlated with the number of large food items brought (as it includes large food items). Repeatability tests on load size (see below) also informed our assessment of the validity of visit rate as a measure of food delivery.

Repeatability Analysis

For this analysis, we first summarised provisioning data for each carer in each recorded hour during which it was observed, including the number of feeding visits of each size class, carer status (individual identity, parent/helper, sex, adult/juvenile) and context variables (date, time, brood size, nestling age, nest helped/unhelped). We retained data from four individuals who were observed during one observation period only, to contribute to estimating between-individual variation. We removed data from three nests at which nestlings were not sexed due to early mortality or inaccessibility, as brood sex ratio affects investment by carers (N. Khwaja and S. A. J. Preston, unpublished). We then calculated within-individual repeatability of visit rate and load size using a Bayesian generalised linear mixed-effects model (GLMM) approach in the MCMCglmm package (Hadfield, 2010). Visit rate was modelled using a Poisson error structure with number of feeding visits as the response variable. Load size was modelled using a binomial error structure with a two-column response variable: number of large food items brought and number of other food items brought (successes and failures respectively in statistical terms). This allowed the proportion of large food items to be examined with appropriate weight given to their total number of visits over the hour (Crawley, 2007). We concentrated on the proportion of large food items because it was less likely to be misidentified than medium-sized food, and less likely to be missed altogether than small food.

Repeatability is calculated as the proportion of variance in a GLMM that is accounted for by the random effect of interest, in this case individual identity. To calculate agreement repeatability (R), we fitted no fixed terms other than the intercept, and included only the identity term as a random effect. We also calculated adjusted repeatability (R_{adj}), which controls for the effect of confounding variables on repeatability and is thus a more valid measure (Nakagawa and Schielzeth, 2010; Debeffe et al., 2015). We included number of nestlings (integer), nestling age (integer: in days), individual status (factor: parent or helper), nest status (factor: helped or unhelped), sex of carer (factor), brood sex ratio (continuous: proportion of males in the nest), date (integer: number of days since 1st September) and time (integer: number of hours since 0700 h) as fixed effects and territory identity as an additional random effect. We initially included season (2012-2013, 2013-2014 or 2014-2015) as an additional random effect, reasoning that it may have influenced the abundance and type of food available, but dropped this term from the model as it explained a negligible amount of variation that could not be accurately estimated, presumably because of similar climatic conditions across seasons. Continuous and integer predictors were scaled and centred. We extracted posterior mode and 50% and 95% credibility intervals of repeatability from the models using the equations for GLMM-based repeatability outlined by Nakagawa and Schielzeth (2010). We present both R and R_{adj} here to illustrate differences between these measures.

Other Factors Affecting Visit Rate and Load Size

We assessed the contribution of factors beyond individual ID (brood size, nestling age, carer status, nest status, carer age, carer sex, brood sex ratio, date, time and territory) to the provisioning behaviour of carers using posterior modes and credibility intervals from fixed effects in the same models used above to estimate R_{adj}.

Testing for Alternation by Carers

As well as the factors mentioned above, within-individual plasticity in parental care can arise from carers responding to the behaviour of their social partner(s) through real-time negotiation over care (Lessells and McNamara, 2012; Johnstone et al., 2014). We tested this hypothesis by looking for non-random patterns of alternation (turn-taking) between nest visits by different carers, which would indicate that carers are responding to each other. We only included provisioning data from day 12 onwards to avoid conflation of feeding visits with brooding. For this analysis, provisioning data collected from 22 nests between 2008 and 2011 were added, in which visits to the nest were recorded in the same way as in 2012-2015 but without information on load size.

We tested whether sequences of visits showed non-random patterns using a custom *k*-category runs test implemented in R, based on equations in Sheskin (2011). This computes whether a sequence shows more or fewer runs of the same value than expected by chance, in this case visits by an individual bird. The sequences we tested were the identity of carers at all feeding visits for each nest, recorded from day 12 onwards. This required concatenating data together such that some consecutive data points did not correspond to true consecutive visits (e.g. the last visit on day 12 followed by the first visit on day 15). As these false steps occurred a maximum of 4 times per sequence, and sequences were on average 122 visits long, we assumed that they did not have a significant influence on our results.

Ethical Note

All captures and ringing were carried out in accordance with New Zealand law, under approval from the University of Canterbury’s Animal Ethics Committee and the New Zealand Department of Conservation (national permit number NM-34956-FAU). Birds were handled only for ringing, measurements and the collection of blood and preen wax samples, which were used in other studies. All adults were released at the capture location within 45 minutes of initial capture, and all nestlings were carefully replaced in their nest.

RESULTS

In total, we collected data from 355 observation periods of 46 different carers provisioning at 33 nests between 2012 and 2015. This encompassed 301 observations of breeder provisioning and 54 observations of helper provisioning. Carers brought an overall mean of 10.84 ± 0.39 SE food items per hour, and 23% of all food items delivered were categorised as large.

Relationship Between Visit Rate and Load Size

We tested the relationship between visit rate and load size across all recorded observation periods. We observed a moderate positive relationship between the number of large and non-large food items brought by each carer in each observation period (Spearman's rank correlation test: $r_s = 0.392$, $N = 355$, $P < 0.001$; Figure 1). This indicates that provisioning riflemen do not trade off visiting frequently with bringing larger food.

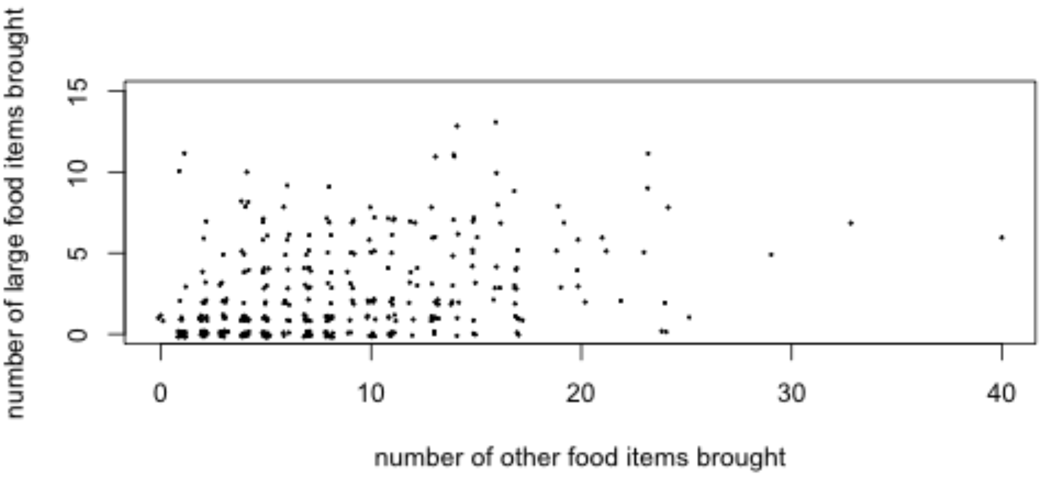

Figure 1 The relationship between the number of large food items and the number of other food items brought during each recorded carer provisioning hour (see Results).

Repeatability of Visit Rate and Load Size

We calculated repeatability of visit rate and load size using data from a total of 338 observation periods for 46 individuals (26 males and 20 females) feeding broods on 14 different territories. *R* was moderate for visit rate and low for load size; however, adjusting for confounding variables gave lower estimates of repeatability for both parameters, notably visit rate (Figure 2).

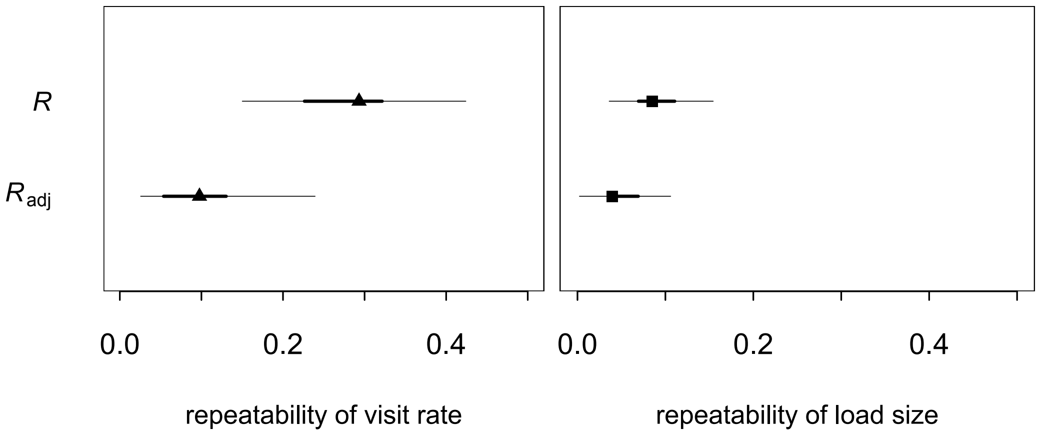

Figure 2 Estimates of agreement (*R*) and adjusted repeatability (R_{adj}) for visit rate and load size (the proportion of large food brought to nestlings) in provisioning riflemen, derived from MCMC generalised linear mixed-effects models. Points show the posterior mode of repeatability estimates, with bold lines spanning 50% credibility intervals (CI) and narrow lines spanning 95% CI. *R* was estimated from models including a random individual identity term and the population intercept as the only fixed term; R_{adj} was estimated from models including a number of confounding variables along with individual identity (see methods).

Other Factors Affecting Visit Rate and Load Size

Fixed effect estimates from GLMMs evaluating the factors influencing visit rate and load size are summarised in Figure 3. Carers made more visits and brought larger food with increased brood size and nestling age, indicating a response to brood demand. Similarly, more visits were made to female-biased broods, which given the larger size of female nestlings is also likely to be a response to brood demand. Helpers made fewer visits to nests than breeders, and males tended to make more visits than females, but brought a lower proportion of large food (though 95% CIs for these estimates overlap zero). The proportion of large food loads decreased later in the day.

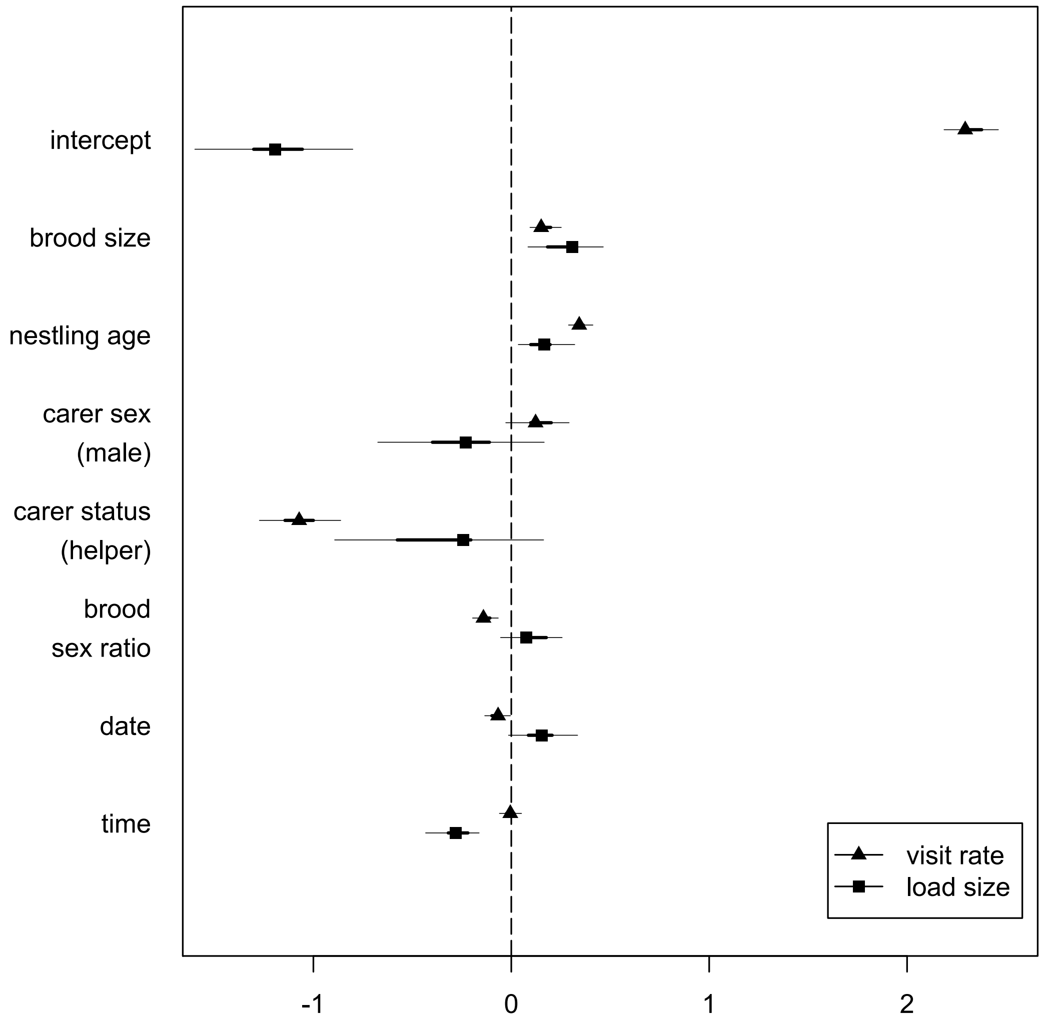

Figure 3 Fixed effect estimates from MCMC generalised linear mixed-effects models explaining variation in visit rate and load size (the proportion of large food brought to nestlings) in provisioning riflemen. Points show the posterior mode of parameter effect sizes, with bold lines spanning 50% credibility intervals (CI) and narrow lines spanning 95% CI. All estimates for visit rate and load size respectively are derived from the same models. Territory identity and individual identity were included as random effects in both models.

Alternation of Nest Visits

We analysed visit sequences at 54 nests (mean = 122 ± 8 SE visits per nest) using runs tests to assess patterns of randomness (Figure 4). There was little evidence for non-random visit sequences in either direction (carers taking turns more or less than expected): 23 nests showed a greater tendency for alternation than expected by chance (3 statistically significant at the 0.05 level), while 31 showed a lower tendency for alternation than expected by chance (1 statistically significant). The handful of 'significant' results are likely to represent false positives caused by multiple testing.

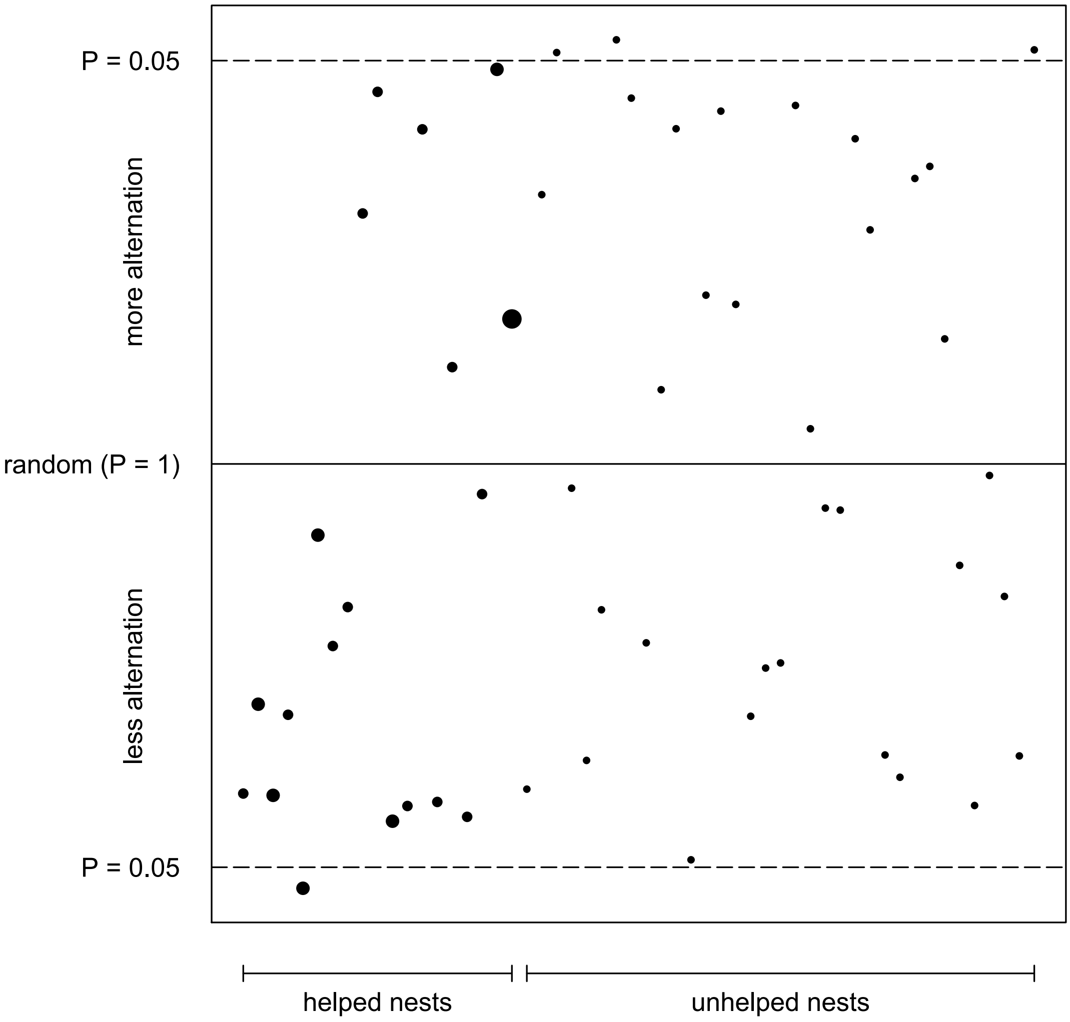

Figure 4 Results from runs tests for randomness carried out on sequences of rifleman visit data. Each point represents the probability for a given nest that visits occurred in

a random order and therefore that sequences were not affected by carers responding to each other's provisioning visits. Points above the random line correspond to nests at which there were more runs by the same individual (more alternation) than expected by chance, and points below correspond to nests with fewer runs (less alternation). Point size represents the number of individuals provisioning at a nest (three, four or six at helped nests and two at each unhelped nest).

DISCUSSION

Our results indicate that visit rate is a valid measure of carer investment in riflemen, as it correlated positively with the proportion of large food delivered to nestlings. This suggests carers visiting more made a genuinely greater contribution to food delivery. Visit rate and load size showed low within-individual repeatability when we accounted for confounding variables. Both measures of investment also increased with brood demand (nestling age and brood size), and visit rate was higher in female-biased clutches. Despite the flexibility indicated by the low repeatability of visit rate, carers showed little evidence of responding to each other's visits.

We assessed the validity of visit rate as a measure of parental investment in riflemen by examining its relationship with load size. Visit rate is the most commonly used measure of parental investment in nesting birds, but its value as a measure may be compromised where carers compensate for making fewer visits by bringing larger food items (Schwagmeyer and Mock, 2008). We found no evidence for this in riflemen; in fact bringing more large food items was positively correlated with bringing more food items of other sizes.

Another potential confound of calculating carer investment from visit rate arises if carers consistently bring food items of the same size: those consistently bringing larger food would have their contribution underestimated by visit rate alone. Sherley (1990) found little evidence for non-random patterns of load sizes in provisioning riflemen, but did not assess between-individual differences. Here, we found repeatability of load size in provisioning riflemen to be low ($R_{\mathrm{adj}} = 0.041$). Taken together, our results strongly support visit rate as a useful measure of parental investment in riflemen. In this regard riflemen align with house finches, in which visit rate almost perfectly predicts weight gain in a nest (Nolan et al., 2001), and chestnut-crowned babblers, in which visit rate is the best predictor of the total amount of food provided (Browning et al., 2012).

While we calculated a moderate estimate of agreement repeatability for carers' visit rates ($R = 0.293$), this shrank to a much lower value ($R_{\mathrm{adj}} = 0.098$) when adjusted for confounding variables. This illustrates that inflated estimates of R can arise as artefacts of brood size, status and sex, rather than differences between individuals in the character of interest. Measures of the repeatability of provisioning behaviour from previous studies are summarised in Table 1, illustrating both the surprising paucity of repeatability studies, and the variety of methods used to calculate R and R_{adj}, which makes comparison between studies challenging. Some high estimates of R could have resulted from a lack of confounding factors included in calculations (Freeman-Gallant and Rothstein, 1999; MacColl and Hatchwell, 2003). However, as a number of studies have controlled for confounds, it appears likely that there is a genuine continuum from highly repeatable, fixed-investment parental care such as that observed in male house sparrows (Schwagmeyer and Mock, 2003; Nakagawa et al., 2007), through the moderate between-individual variation of long-tailed tits (Adams et al., 2015), to species like riflemen in which repeatability is low and parental care highly flexible.

Table 1 Summary of studies investigating repeatability of parental care in provisioning birds. Repeatability of visit rate is presented unless stated otherwise. *R* is agreement repeatability, in which no confounding variables are controlled. R_{adj} is adjusted repeatability, where the factors controlled are given in the adjacent column. Asterisks denote estimates based on within-year data rather than across multiple years. Abbreviations for methods: ANOVA = analysis of variance; BLMM = Bayesian linear mixed-effects model; DEE = daily energy expenditure; LMM = linear mixed-effects model; MCMCglmm = Markov chain Monte Carlo generalised linear mixed-effects model. Abbreviations for adjusted factors: a = carer age; bs = brood size; d = date; #h = number of helpers at nest; mf = sex; na = nestling age; pa = partner age; pe = partner effort (visit rate); sr = brood sex ratio; st = status (breeder/helper); t = time.

Species	**Study**	**Method**	***R***	**R_{adj}**	**Adjusted factors**
Manx shearwater (*Puffinus puffinus*)	Gray et al. (2005)	One-way ANOVA on g/day (by pair)	0.02		
Savannah sparrow (*Passerculus sandwichensis*)	Freeman-Gallant and Rothstein (1999)	One-way ANOVA	♂ 0.60 ♀ 0.19		
House sparrow (*Passer domesticus*)	Schwagmeyer and Mock (2003)	ANOVA*	♂ 0.38 ♀ -0.06	♂ 0.44 ♀ 0.08	bs, d
	Nakagawa et al.	LMM*	♂ 0.58	♂ 0.63	bs

	(2007)		♀ 0.28	♀ 0.27	
	Dor and Lotem (2010)	One-way ANOVA	♂ 0.51 ♀ 0.57		
	Cleasby et al. (2013)	BLMM		♂ 0.23 ♀ 0.33	a, bs, d, na, pa, pe
Long-tailed tit (*Aegithalos caudatus*)	MacColl and Hatchwell (2003)	One-way ANOVA	♂ 0.70 ♀ 0.37		
	Adams et al. (2015)	Animal model*		0.24	bs, #h, mf, na, st
Pied flycatcher (*Ficedula hypoleuca*)	Potti et al. (1999)	One-way ANOVA on DEE	♂ -0.21 ♀ 0.64		
Stitchbird (*Notiomystis cincta*)	Low et al. (2012)	LMM*		♂ 0.19 ♀ 0.02	bs, na
Rifleman (*Acanthisitta chloris*)	This study	MCMCglmm	0.29	0.10	bs, d, mf, na, sr, st, t

High repeatability of visit rate has been regarded as consistent with sealed-bid models of investment, in which investment is fixed over an individual's lifetime but subject to selection across generations (Houston and Davies, 1985; Nakagawa et al., 2007). At the opposite end of the continuum are systems in which individuals are highly flexible in their investment; specifically, their investment is strongly influenced by their social partners (McNamara et al., 1999; Schwagmeyer et al., 2002; Hinde and Kilner, 2007). Recent theoretical and empirical work suggests that alternating visits to nestlings (taking turns) is a simple way by which negotiation over care can be regulated, and is associated with improved rates of food delivery and greater reproductive success (Johnstone et al., 2014; Bebbington and Hatchwell, 2016). Although theoretical predictions of alternation have so far been limited to biparental systems, models suggest that basic investment rules are readily extendable to cooperative groups

(Savage et al., 2012, 2013, 2015), and data from cooperative groups of chestnut-crowned babblers show patterns associated with active turn-taking by carers (Savage, 2014). In contrast, our analysis did not support the hypothesis that rifleman carers take turns feeding nestlings, or visit in any other non-random pattern. This was the case for both helped and unhelped nests. The lack of turn-taking in riflemen, despite its presence in other species, may be attributable to low sexual conflict. Negotiation represents a stable solution to conflict over parental care, which arises from the divergent evolutionary interests of carers, who each fare better if others work harder. However, such conflict is diminished in riflemen, where there is no divorce (although adults will re-pair if their partner dies) and no recorded extra-pair paternity (Preston et al., 2013). In a system without divorce, partners improve their fitness by exploiting one another only if the other dies; exploitation is therefore a risky strategy because it will presumably be detrimental to breeding success in the event that a partner survives in poor condition. Riflemen thus appear closer to 'true' monogamy (with no conflict) than many comparable systems (Parker, 1985). Theoretical work to date has generally assumed conflict between partners, and focused on the resolution of this conflict (e.g Houston and Davies, 1985; McNamara et al., 1999; Johnstone et al., 2014). We would welcome an examination of how low conflict between carers affects the predicted behavioural outcomes of investment games.

In conclusion, we have combined analyses of repeatability, negotiation and other factors affecting parental behaviour to show that riflemen invest flexibly in offspring, but do not respond to each other's investment by taking turns. Instead, individuals vary their provisioning in response to their brood's demand and their own breeding status. Low sexual conflict might lead to systems like riflemen exhibiting both low partner responsiveness and highly flexible investment. Our results demonstrate the range of questions that can be answered using provisioning data, and how some results inform our interpretation of others. We suggest that future studies should consider possible confounds before drawing conclusions from raw measures of visit rates, especially in species with highly variable social and environmental contexts of care.

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