Flexibility but no coordination of visits in provisioning riflemen

Nyil Khwaja [a, *], Stephanie A. J. Preston [a], Ben J. Hatchwell [a], James V. Briskie [b], Isabel S. Winney [a, c], James L. Savage [d]

[a] Department of Animal & Plant Sciences, University of Sheffield, Sheffield, U.K.
[b] School of Biological Sciences, University of Canterbury, Christchurch, New Zealand
[c] Max Planck Institute for Ornithology, Seewiesen, Germany
[d] Department of Animal Sciences, Wageningen UR, The Netherlands

ARTICLE INFO

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 riflemen were 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, 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.

© 2017 The Authors. Published by Elsevier Ltd on behalf of The Association for the Study of Animal Behaviour. This is an open access article under the CC BY license (http://creativecommons.org/licenses/by/4.0/).

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 babblers, *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

* Correspondence: N. Khwaja, Department of Animal & Plant Sciences, University of Sheffield, Western Bank, Sheffield S10 2TN, U.K.
E-mail address: bop12nk@shef.ac.uk (N. Khwaja).

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; Ghalambor, 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 babblers (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 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 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). Riflemen 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 riflemen. 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 riflemen 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 kānuka, 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). 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 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). 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 analyses presented here, nonfeeding visits were removed from the data. All statistical analyses were implemented in R 3.2.2 (R Development Core Team, Vienna, Austria).

Testing the Relationship Between Visit Rate and Load Size

We examined the relationship between load size and visit rate using a Spearman rank correlation test, by comparing the number of visits and the proportion of large food items brought by each individual for each recorded hour. If carers that infrequently visit compensate by bringing larger food, we would expect a negative relationship between these two variables. 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 summarized 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/ not helped). We retained data from four individuals that 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 (Khwaja, 2017). We then calculated within-individual repeatability of visit rate and load size using a Bayesian generalized 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 large food items because they were 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 explained 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 factors on the response variable and is thus a more valid measure (Debeffe et al., 2015; Nakagawa & Schielzeth, 2010). We included number of nestlings (integer), nestling age (integer: in days), individual status (factor: parent or helper), nest status (factor: helped or not helped), sex of carer (factor), brood sex ratio (continuous: proportion of males in the nest), date (integer: number of days since 1 September) and time (integer: number of hours after 0700 hours) 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 (CIs) 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 identity (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 CIs 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 (Johnstone et al., 2014; Lessells & McNamara, 2012). We tested this hypothesis by looking for nonrandom 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 nonrandom 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 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 four 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 min of initial capture, and all nestlings were carefully replaced in their nest.

RESULTS

In total, we collected data from 355 observation periods of 46 unique carers provisioning at 33 nests between 2012 and 2015. This encompassed 301 observation periods of breeder provisioning and 54 observation periods of helper provisioning. Carers brought an overall mean of 10.84 ± 0.39 SE food items/h, and 23% of all food items delivered were categorized as large. Of the 46 carers, seven were recorded acting as breeders and helpers at different broods.
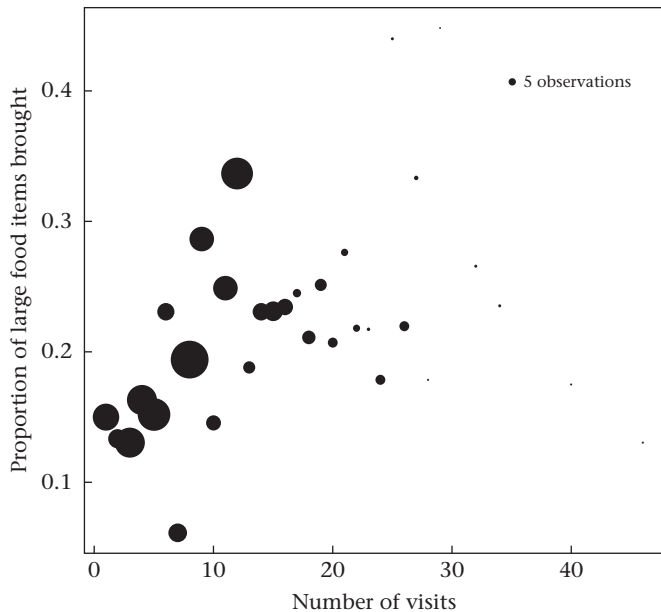
Figure 1. The relationship between the number of provisioning visits and the proportion of large food items brought during each recorded carer provisioning hour. Points represent the mean proportion of large food items brought for each number of visits, weighted by sample size.

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 visits and the proportion of large food items brought by each carer in each observation period (Spearman rank correlation test: $r_s = 0.323$, $N = 355$, $P < 0.001$; Fig. 1). This indicates that provisioning riflemen do not trade off visiting frequently with bringing larger food items; in fact, those visiting more frequently also generally brought a greater proportion of large items.

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 unique 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 (Fig. 2).

Other Factors Affecting Visit Rate and Load Size

Fixed-effect estimates from GLMMs evaluating the factors influencing visit rate and load size are summarized in Fig. 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 (although 95% CIs for these estimates overlap zero). The proportion of large food loads decreased later in the day.

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 (Fig. 4). There was little evidence for nonrandom 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 (three statistically significant at the 0.05 level), while 31 showed a lower tendency for alternation than expected by chance (one statistically significant). The handful of 'significant' results are likely to represent false positives caused by multiple testing.

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 also increased with brood demand (nestling age and brood size), although only 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.
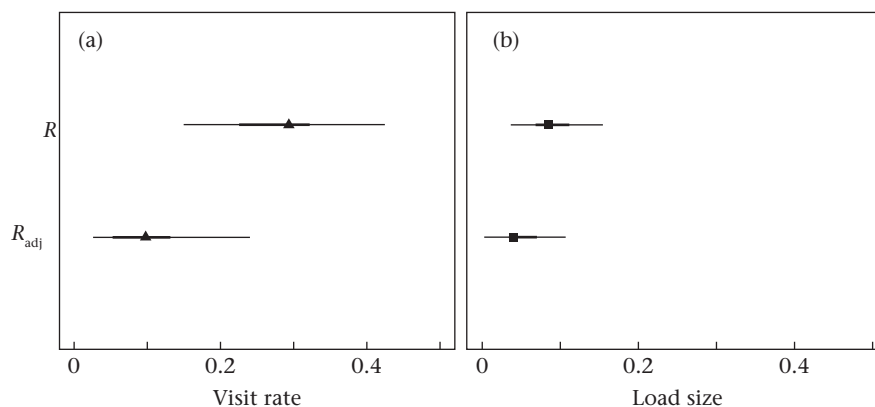

Figure 2. Estimates of agreement (R) and adjusted repeatability (R_{adj}) for (a) visit rate and (b) load size (the proportion of large food brought to nestlings) in provisioning riflemen, derived from MCMC generalized linear mixed-effects models. Points show the posterior mode of repeatability estimates, 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.
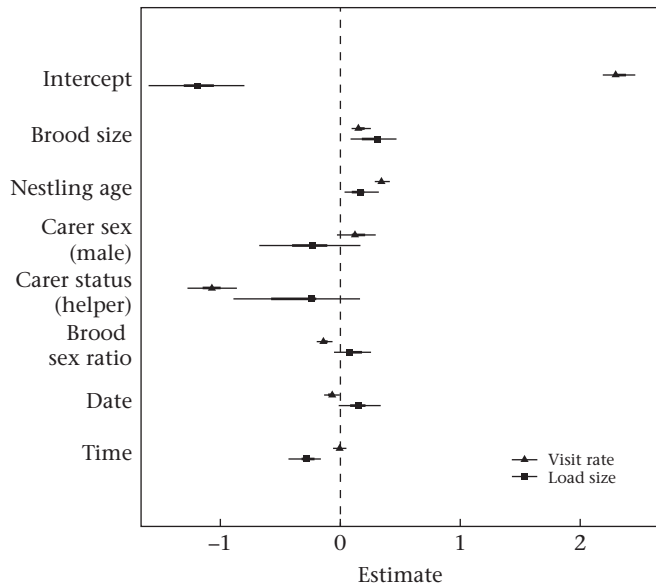
Figure 3. Fixed-effect estimates from MCMC generalized linear mixed-effects models explaining variation in visit rate and load size (the proportion of large food brought to nestlings) in provisioning riflemen. Points show the posterior mode of parameter effect estimates, with bold lines spanning 50% 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.

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
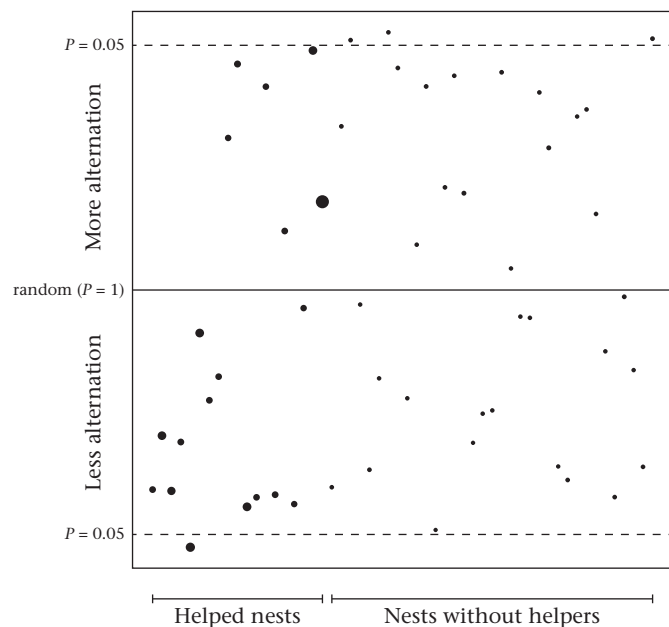

Figure 4. Results from runs tests for randomness carried out on sequences of rifleman visit data. Each point represents the probability for a given nest that visits occurred in a random order and therefore that sequences were not affected by carers responding to each other's provisioning visits. Points 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 nest without helpers).

compromised where carers compensate for making fewer visits by bringing larger food items (Schwagmeyer & Mock, 2008). We found no evidence for this in riflemen; in fact, visiting more often was positively correlated with bringing a greater proportion of large food items.

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 nonrandom 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 ($R_{adj} = 0.041$). 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 ($R_{adj} = 0.098$) 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 summarized 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 & Rothstein, 1999; MacColl & 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 (Nakagawa et al., 2007; Schwagmeyer & Mock, 2003), through the moderate between-individual variation of long-tailed tits (Adams, Robinson, Mannarelli, & Hatchwell, 2015), to species like riflemen in which repeatability is low and parental care highly flexible.

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 & 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 (Hinde & Kilner, 2007; McNamara et al., 1999; Schwagmeyer et al., 2002). 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 (Bebbington & Hatchwell, 2016; Johnstone et al., 2014). Although theoretical predictions of alternation have so far been limited to biparental systems, models suggest that individual investment rules lead to similar predictions when extended to cooperative groups (Johnstone, 2011; Savage, Russell, & Johnstone, 2012, 2013, 2015), and data from cooperative groups of chestnut-crowned babblers show patterns suggestive of 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 nonrandom pattern. This was the case for both helped nests and nests without helpers.

The lack of turn taking in riflemen, despite its presence in other species, may be attributable to low levels of sexual conflict.

Table 1
Summary of studies investigating repeatability of parental care in provisioning birds

Species	Study	Method	R	R_{adj}	Adjusted factors
Manx shearwater, *Puffinus puffinus*	Gray, Brooke, and Hamer (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. (2007)	LMM*	♂ 0.58 ♀ 0.28	♂ 0.63 ♀ 0.27	BS
	Dor and Lotem (2010)	One-way ANOVA	♂ 0.51 ♀ 0.57		
	Cleasby, Nakagawa, and Burke (2013)	BLMM		♂ 0.23 ♀ 0.33	CA, 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
European starling, *Sturnus vulgaris*	Fowler and Williams (2015)	LMM	♀ 0.04	♀ 0.34	BS
Pied flycatcher, *Ficedula hypoleuca*	Potti, Moreno, and Merino (1999)	One-way ANOVA on DEE	♂ −0.21 ♀ 0.64		
Stitchbird, *Notiomystis cincta*	Low, Makan, and Castro (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

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. ANOVA = analysis of variance; BLMM = Bayesian linear mixed-effects model; DEE = daily energy expenditure; LMM = linear mixed-effects model; MCMCglmm = Markov chain Monte Carlo generalized linear mixed-effects model. CA = carer age; BS = brood size; D = date; H = number of helpers at the nest; MF = sex; NA = nestling age; PA = partner age; PE = partner effort (visit rate); SR = brood sex ratio; ST = status (breeder/helper); T = time.

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 extrapair paternity (Preston et al., 2013). In a system without divorce, exploitation is a risky strategy because it will presumably be detrimental to breeding success if 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 has focused on the resolution of this conflict (e.g. Houston & Davies, 1985; Johnstone et al., 2014; McNamara et al., 1999). Further theoretical work is needed to examine 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. We hypothesize that low sexual conflict might lead to species like riflemen exhibiting both low partner responsiveness and highly flexible investment, as there is less scope for exploitation. 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.

References

Adams, M. J., Robinson, M. R., Mannarelli, M.-E., & Hatchwell, B. J. (2015). Social genetic and social environment effects on parental and helper care in a cooperatively breeding bird. *Proceedings of the Royal Society B: Biological Sciences, 282*, 20150869.

Bebbington, K., & Hatchwell, B. J. (2016). Coordinated parental provisioning is related to feeding rate and reproductive success in a songbird. *Behavioral Ecology, 27*, 652–659.

Bell, A. M., Hankinson, S. J., & Laskowski, K. L. (2009). The repeatability of behaviour: A meta-analysis. *Animal Behaviour, 77*, 771–783.

Bowers, E. K., Nietz, D., Thompson, C. F., & Sakaluk, S. K. (2014). Parental provisioning in house wrens: Effects of varying brood size and consequences for offspring. *Behavioral Ecology, 25*, 1485–1493.

Brouwer, L., Van de Pol, M., & Cockburn, A. (2014). The role of social environment on parental care: Offspring benefit more from the presence of female than male helpers. *Journal of Animal Ecology, 83*, 491–503.

Browning, L. E., Young, C. M., Savage, J. L., Russell, D. J. F., Barclay, H., Griffith, S. C., et al. (2012). Carer provisioning rules in an obligate cooperative breeder: Prey type, size and delivery rate. *Behavioral Ecology and Sociobiology, 66*, 1639–1649.

Cleasby, I. R., Nakagawa, S., & Burke, T. (2013). Providing chicks with extra food lowers male but not female provisioning in the house sparrow *Passer domesticus*. *Ibis, 155*, 857–866.

Crawley, M. J. (2007). *The R book*. Chichester, U.K.: J. Wiley.

Crick, H. Q. P. (1992). Load-lightening in cooperatively breeding birds and the cost of reproduction. *Ibis, 134*, 56–61.

Dall, S. R. X., Houston, A. I., & McNamara, J. M. (2004). The behavioural ecology of personality: Consistent individual differences from an adaptive perspective. *Ecology Letters, 7*, 734–739.

Davies, N. B. (1986). Reproductive success of dunnocks, *Prunella modularis*, in a variable mating system. I. Factors influencing provisioning rate, nestling weight and fledging success. *Journal of Animal Ecology, 55*, 123–138.

Debeffe, L., Lemaître, J. F., Bergvall, U. A., Hewison, A. J. M., Gaillard, J. M., Morellet, N., et al. (2015). Short- and long-term repeatability of docility in the roe deer: Sex and age matter. *Animal Behaviour, 109*, 53–63.

Dor, R., & Lotem, A. (2010). Parental effort and response to nestling begging in the house sparrow: Repeatability, heritability and parent-offspring conflict. *Journal of Evolutionary Biology, 23*, 1605–1612.

Fowler, M. A., & Williams, T. D. (2015). Individual variation in parental workload and breeding productivity in European starlings: Is the effort worth it? *Ecology and Evolution, 5*, 3585–3599.

Freeman-Gallant, C. R., & Rothstein, M. D. (1999). Apparent heritability of parental care in savannah sparrows. *Auk, 116*, 1132–1136.

Ghalambor, C. K., Peluc, S. I., & Martin, T. E. (2013). Plasticity of parental care under the risk of predation: How much should parents reduce care? *Biology Letters, 9*, 20130154.

Gill, B. J. (1980). Abundance, feeding, and morphology of passerine birds at Kowhai Bush, Kaikoura, New Zealand. *New Zealand Journal of Zoology, 7*, 235–246.

Gray, C. M., Brooke, M. D. L., & Hamer, K. C. (2005). Repeatability of chick growth and food provisioning in Manx shearwaters *Puffinus puffinus*. *Journal of Avian Biology, 36*, 374–379.

Hadfield, J. D. (2010). *MCMCglmm: MCMC generalised linear mixed models [R package]*. Retrieved from: https://cran.r-project.org/web/packages/MCMCglmm/index.html.

Hatchwell, B. J. (1999). Investment strategies of breeders in avian cooperative breeding systems. *American Naturalist, 154*, 205–219.

Hinde, C. A., Johnstone, R. A., & Kilner, R. M. (2010). Parent-offspring conflict and coadaptation. *Science, 327*, 1373–1376.

Hinde, C. A., & Kilner, R. M. (2007). Negotiations within the family over the supply of parental care. *Proceedings of the Royal Society B: Biological Sciences, 274*, 53–60.

Houston, A. I., & Davies, N. B. (1985). The evolution of cooperation and life history in the dunnock. In R. M. Sibly, & R. S. Smith (Eds.), *Behavioural ecology* (pp. 471–481). Oxford, U.K.: Blackwell Scientific.

Johnstone, R. A. (2011). Load lightening and negotiation over offspring care in cooperative breeders. *Behavioral Ecology, 22*, 436–444.

Johnstone, R. A., Manica, A., Fayet, A. L., Stoddard, M. C., Rodriguez-Gironés, M. A., & Hinde, C. A. (2014). Reciprocity and conditional cooperation between great tit parents. *Behavioral Ecology, 25*, 216–222.

Khwaja, N. (2017). *Investment patterns and kinship cues in a cooperatively breeding bird* (Doctoral thesis). Sheffield, U.K.: University of Sheffield.

Kilner, R. M., Madden, J. R., & Hauber, M. E. (2004). Brood parasitic cowbird nestlings use host young to procure resources. *Science, 305*, 877–879.

Koenig, W. D., & Walters, E. L. (2016). Provisioning patterns in the cooperatively breeding acorn woodpecker: Does feeding behaviour serve as a signal? *Animal Behaviour, 119*, 124–134.

Lessells, C. M., & McNamara, J. M. (2012). Sexual conflict over parental investment in repeated bouts: Negotiation reduces overall care. *Proceedings of the Royal Society B: Biological Sciences, 279*, 1506–1514.

Low, M., Makan, T., & Castro, I. (2012). Food availability and offspring demand influence sex-specific patterns and repeatability of parental provisioning. *Behavioral Ecology, 23*, 25–34.

MacColl, A. D. C., & Hatchwell, B. J. (2003). Heritability of parental effort in a passerine bird. *Evolution, 57*, 2191–2195.

McNamara, J. M., Gasson, C. E., & Houston, A. I. (1999). Incorporating rules for responding into evolutionary games. *Nature, 401*, 368–371.

Naef-Daenzer, B., & Keller, L. F. (1999). The foraging performance of great and blue tits (*Parus major* and *P. caeruleus*) in relation to caterpillar development, and its consequences for nestling growth and fledging weight. *Journal of Animal Ecology, 68*, 708–718.

Nakagawa, S., Gillespie, D. O. S., Hatchwell, B. J., & Burke, T. (2007). Predictable males and unpredictable females: Sex difference in repeatability of parental care in a wild bird population. *Journal of Evolutionary Biology, 20*, 1674–1681.

Nakagawa, S., & Schielzeth, H. (2010). Repeatability for Gaussian and non-Gaussian data: A practical guide for biologists. *Biological Reviews, 85*, 935–956.

Nam, K.-B., Simeoni, M., Sharp, S. P., & Hatchwell, B. J. (2010). Kinship affects investment by helpers in a cooperatively breeding bird. *Proceedings of the Royal Society B: Biological Sciences, 277*, 3299–3306.

Nolan, P. M., Stoehr, A. M., Hill, G. E., & McGraw, K. J. (2001). The number of provisioning visits by house finches predicts the mass of food delivered. *Condor, 103*, 851–855.

Parker, G. A. (1985). Models of parent-offspring conflict. V. Effects of the behaviour of the two parents. *Animal Behaviour, 33*, 519–533.

Potti, J., Moreno, J., & Merino, S. (1999). Repeatability of parental effort in male and female pied flycatchers as measured with doubly labeled water. *Canadian Journal of Zoology, 77*, 174–179.

Preston, S. A. J., Briskie, J. V., Burke, T., & Hatchwell, B. J. (2013). Genetic analysis reveals diverse kin-directed routes to helping in the rifleman *Acanthisitta chloris*. *Molecular Ecology, 22*, 5027–5039.

Preston, S. A. J., Briskie, J. V., & Hatchwell, B. J. (2016). Adult helpers increase the recruitment of closely related offspring in the cooperatively breeding rifleman. *Behavioral Ecology, 27*, 1617–1626.

Savage, J. L. (2014). *Maternal investment tactics in cooperative breeding systems* (Doctoral thesis). Cambridge, U.K.: University of Cambridge.

Savage, J. L., Russell, A. F., & Johnstone, R. A. (2012). Maternal costs in offspring production affect investment rules in joint rearing. *Behavioral Ecology, 24*, 750–758.

Savage, J. L., Russell, A. F., & Johnstone, R. A. (2013). Intra-group relatedness affects parental and helper investment rules in offspring care. *Behavioral Ecology and Sociobiology, 67*, 1855–1865.

Savage, J. L., Russell, A. F., & Johnstone, R. A. (2015). Maternal allocation in cooperative breeders: Should mothers match or compensate for expected helper contributions? *Animal Behaviour, 102*, 189–197.

Schwagmeyer, P. L., & Mock, D. W. (2003). How consistently are good parents good parents? Repeatability of parental care in the house sparrow, *Passer domesticus*. *Ethology, 109*, 303–313.

Schwagmeyer, P. L., & Mock, D. W. (2008). Parental provisioning and offspring fitness: Size matters. *Animal Behaviour, 75*, 291–298.

Schwagmeyer, P. L., Mock, D. W., & Parker, G. A. (2002). Biparental care in house sparrows: Negotiation or sealed bid? *Behavioral Ecology, 13*, 713–721.

Sherley, G. A. (1990). Relative costs and benefits of co-operative breeding to riflemen (*Acanthisitta chloris*) parents. *Behaviour, 112*, 1–22.

Sherley, G. A. (1993). Parental investment, size sexual dimorphism, and sex ratio in the rifleman (*Acanthisitta chloris*). *New Zealand Journal of Zoology, 20*, 211–217.

Sheskin, D. J. (2011). *Handbook of parametric and nonparametric statistical procedures*. Boca Raton, FL: CRC Press.

Smith, B. R., & Blumstein, D. T. (2008). Fitness consequences of personality: A meta-analysis. *Behavioral Ecology, 19*, 448–455.

Trivers, R. L. (1972). Parental investment and sexual selection. In B. Campbell (Ed.), *Sexual selection and the descent of man* (pp. 139–179). Chicago, IL: Aldine.

Trivers, R. L. (1974). Parent-offspring conflict. *American Zoologist, 14*, 249–264.

Withers, S. (2013). Rifleman. In C. M. Miskelly (Ed.), *New Zealand birds online* [online]. Retrieved from: http://nzbirdsonline.org.nz/species/rifleman.