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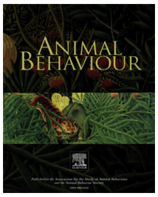

A sequential collective action game and its applications to cooperative parental care in a songbird

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Collective action problems arise when two or more individuals can free ride on one another's efforts when investing jointly in a common good. Many collective action tasks in nature, such as parental care, require multiple stages of investments to complete a task, but how the costs of consecutive periods of investment and the excludability and diminishability of a collective good influence investment strategy remains poorly understood. Here, we first developed an evolutionary game-theoretical model to explore the theoretical consequences of sequential investment strategies in collective good problems. We then investigated cooperative parental care during both incubation and provisioning stages in the joint-nesting Taiwan yuhina, *Yuhina brunneiceps*, to test the key theoretical predictions of the model. We found that yuhina females that laid eggs earlier than other females invested more than they did in incubation (the first stage in the collective action problem). Intriguingly, but as predicted by our model, females that laid eggs earlier brought less food to nestlings in the joint brood during the nestling provisioning stage (the second stage in the collective action problem). This seemingly puzzling pattern can be explained by the fact that females that laid eggs earlier started incubation earlier and continued incubating eggs, which led to their offspring hatching earlier and being competitively superior (obtaining more food) at the nestling provisioning stage. Our study highlights the importance of understanding the complex nature of investment strategies parsed over different development stages in collective action problems.
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A collective action problem (CAP) arises when group benefits are available to every group member, but only cooperators pay the cost of creating such benefits (Poteete, Janssen, & Ostrom, 2010). CAPs have long been important in the economics literature (Olson, 1965; Sandler, 1992), but have received relatively little attention in evolutionary biology (Brown, 1999; Kummerli et al., 2007; Nunn & Lewis, 2001), even though individuals in many species face CAPs in nature, ranging from cooperative care of young (Yuan, Shen, Lin, & Lee, 2005), cooperative hunting and territory defence (Heinsohn & Packer, 1995; Kleiber, Kyle, Rockwell, & Dickinson, 2007) to predator mobbing (Krams, Krama, Igaune, & Mand, 2008), vigilance (Beauchamp, 2009) and sentinel behaviour (Clutton-Brock et al., 1999; Wright, Berg, De Kort, Khazin, & Maklakov, 2001). One behaviour where CAPS have been studied from an evolutionary perspective is biparental care. Both theoretical and empirical studies have shown that parents face an evolutionary conflict of interest because each parent stands to gain if the other does more of the work (Johnstone et al., 2014; Royle, Hartley, & Parker, 2002). Studies of biparental care have found that this conflict of collective investment in parental care causes parents to reduce their effort below that which would maximize their total fitness payoff (Houston & Davies, 1985; Lessells & McNamara, 2012; McNamara, Houston, Barta, & Osorno, 2003; Royle et al., 2002).

Many models suggest that heterogeneity within a group is an important factor affecting the outcome of CAPs (Olson, 1965; Poteete & Ostrom, 2004; Sandler, 1992). These models propose that in heterogeneous groups ‘advantaged’ individuals, such as individuals in better body condition and individuals with higher ranking, will contribute more to the collective good because they

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can gain higher benefits and/or suffer lower costs than other group members (Frank, 2010; Olson, 1965; Sandler, 1992). Indeed, numerous empirical studies have shown that advantaged individuals contribute more to creating benefits that are shared by group members (Dixon, Ross, O'Malley, & Burke, 1994; Nunn, 2000; Packer, 1988).

A rarely considered, but potentially important aspect of collective action problems is that multiple stages of investments are often necessary to complete a task. As such, the costs and benefits of investing in one stage might depend on the investment at other stages (Savage, Russell, & Johnstone, 2013). For example, parental investment in birds includes an egg production stage, an incubation stage and a final stage in which nestlings and fledglings are provisioned. A study on cooperatively breeding superb fairy-wrens, *Malurus cyaneus*, has found that mothers adjust their egg-laying strategy if helpers are present by laying smaller eggs of lower nutritional content that produce lighter nestlings. However, helpers feed the nestlings at a higher rate, and compensate fully for such reductions in maternal investment (Russell, Langmore, Cockburn, Astheimer, & Kilner, 2007).

The properties of collective goods may differ across stages. For example, in joint-nesting birds in which more than two individuals provide parental care to the offspring, if individuals have limited abilities to recognize their own eggs, incubation generates a collective good that is nonexcludable, because individuals cannot efficiently exclude others from using the collective good (Quinn, Haselmayer, Dey, & Jamieson, 2012). At this stage of the game, the number of offspring that an individual has in the joint clutch is the key determinant of its share of the collective good. At the next stage of the game, where group members provision food to the nestlings, however, collective goods are potentially excludable, because nestlings could compete for and monopolize the food resources. Consequently, the competitive ability of an individual's offspring can be crucial during the nestling stage.

The general question of how offspring quality and quantity influence investment strategy in collective action problems with multiple stages and different properties (e.g. excludability, diminishability) remains largely overlooked.

Here, we first developed a game-theoretical model to explore the theoretical consequences of sequential investment strategies in collective good games with consecutive stages. We then tested whether unequal benefits (i.e. having more or better quality offspring) are present with respect to parental care in joint-nesting Taiwan yuhinas, *Yuhina brunneiceps*, and if such unequal benefits are present, how they influence cooperative care strategies at different stages. The benefits of joint-nesting behaviour in yuhinas, a species in which two to four genetically unrelated pairs breed together (Yuan, Liu, & Shen, 2004), include the sharing of parental care responsibilities during both incubation and provisioning stages (Shen, Yuan, & Liu, 2016), but co-breeding yuhinas also compete with other group members for egg laying (Shen et al., 2012).

In altricial birds such as yuhinas hatching is often asynchronous, and early hatched nestlings are usually dominant over their younger nestmates (Drummond & Garcia Chavelas, 1989). Females in altricial species that breed communally employ various strategies to facilitate early hatching of their own young. These strategies include tossing the eggs of other group members out of the nest before laying their first egg (Riehl, 2011). Unlike most joint-nesting species, egg tossing rarely occurs in yuhinas (7.0% of clutches, $N = 43$, Shen et al., 2016). An experiment in which model eggs were added to nests also suggests that yuhinas are unable to recognize their own eggs as the model eggs were all incubated for more than 10 days (Shen et al., 2016). Thus, egg tossing is not an important competitive strategy in yuhinas. Instead, individuals ‘tussle’ with one another for the chance to lay more eggs earlier and initiate nocturnal incubation before other individuals, which has the effect of increasing the probability that their eggs hatch first (Shen et al., 2012).

We hypothesized that unequal benefits are possible in co-breeding yuhinas because individuals produce different numbers of young that also differ in competitive abilities. We first examined the behaviours that yuhinas employ during egg laying and offspring hatching sequences to understand their potential strategies for gaining a greater share of the benefits than other group members. We then examined the number and quality of nestlings as measured by body weight and competitive ability. Last, we looked at the role of unequal benefits among group members in influencing investment during the incubation and nestling provisioning stages in yuhinas by investigating the relationship between the quality and quantity of offspring and incubation and provisioning effort.

PARENTAL CARE MODEL AS A TWO-STAGE COLLECTIVE ACTION GAME

Here we model how unequal benefits influence individual investment strategy in a two-stage collective action problem in cooperatively breeding species. For altricial birds, cooperation during breeding may occur during two distinct stages, incubation and nestling provisioning, that have different collective good properties.

We model the situation as a sequential game (Maynard Smith, 1982; McNamara et al., 2003), in which individuals first choose their incubation effort. Following this, all individuals determine their levels of investment in provisioning young, conditional upon their investment in incubation in the first stage. In the incubation stage, we assume parents cannot recognize their own eggs and all eggs are incubated together, as observed in yuhinas (Shen et al., 2012, 2016), and so the cooperative incubation generates nonexcludable and nondiminishable goods (i.e. goods that do not decrease in value when others use them) among group members. We assume all offspring (eggs) have equal fitness during incubation and fitness increases sigmoidally with the total incubation effort of m advantaged individuals (i.e. those individuals in better body condition and/or individuals with higher ranking) and n disadvantaged individuals (i.e. individuals that are not advantaged), given by these functions:

$$V_A[v,v'] = \frac{ke^{a\left(v_A+(n-1)v'_A+mv'_D\right)}}{ke^{a\left(v_A+(n-1)v'_A+mv'_D\right)}+(1-k)} \tag{1a}$$

and

$$V_D[v,v'] = \frac{ke^{a\left(nv'_A+v_D+(m-1)v'_D\right)}}{ke^{a\left(nv'_A+v_D+(m-1)v'_D\right)}+(1-k)}, \tag{1b}$$

where focal advantaged and focal disadvantaged individuals invest v_A and v_D, respectively, and v'_A and v'_D represent the population average levels of incubation efforts for the advantaged and disadvantaged individuals; k and a are scaling factors describing the intercept ($0 < k < 1$) and the shape ($a > 0$), respectively, of the S-shaped offspring fitness function during incubation ($0 < v_A, v_D < 1$).

In the provisioning stage, since the food brought by the group members to the nestlings is both a diminishable good and an excludable good, both the number and quality of offspring (measured in terms of competitive ability) will influence the share of the collective goods at the nestling provisioning stage. We assume advantaged individuals have s_A and disadvantaged

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