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Bayesian estimation of competitiveness in male house finches: small-billed males are more competitive

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A common method for assessing the competitiveness of animals, especially in birds, is to pit pairs of unfamiliar individuals against each other in contests for limited resources under controlled conditions. Although this approach can clarify dominant–subordinate relationships within dyads, it is often difficult to determine competitiveness for a large group of individuals. Here, by using Bayesian statistical inference and 'hypothetical competition groups', which are formed when individuals experience a series of paired contests, we estimated social competitiveness of male house finches, *Haemorhous mexicanus*. First, Bayesian competitiveness estimates from paired contests successfully predicted future contest outcomes among four unfamiliar individuals (i.e. social dominance). When data of all rank combinations were pooled, future dominant males had, on average, higher competitiveness estimates than future subordinate males. Similarly, Bayesian statistical inference and hypothetical competition groups identified accurately the relative competitiveness of four subgroups of males (i.e. colourful and drab males from urban and rural sites), which matched the result of direct contests when they were all put into the same cage. This consistency reinforces the validity of Bayesian competitiveness estimation based on hypothetical competition groups. Moreover, we found that the competitiveness estimate was negatively linked to male beak size in the Bayesian framework. Males with smaller bills were more competitive than those with larger bills, perhaps due to their elevated foraging motivation (i.e. limited ability to consume or husk large, valuable seeds). We argue that Bayesian competitiveness estimations, together with a series of paired contests, is a sophisticated approach for acquiring a broad understanding of social and individual competitiveness.

A classic laboratory method for studying animal competition is to pair two individuals in a contest and let them vie for access to a limited resource. Such dyadic interactions are widely used, especially in birds, for studying dominant–subordinate relationships within a sex (e.g. Koivula, Lahti, Orreli, & Rytkönen, 1993), in the use of status signals (e.g. McGraw & Hill, 2000a,b; Senar, 2006) and during intersexual (e.g. Belthoff & Gowaty, 1996) or interspecific interactions (e.g. Grava et al., 2012). This method is straightforward since each contestant has only one opponent and the number of aggressive encounters won and lost reveals the competitiveness of the focal individual relative to the opponent. However, this relative measure within dyads cannot be interpreted as individual competitiveness in a larger group (i.e. in social species in which group membership is dynamic and multiple individuals can compete). Some studies (e.g. Gonzalez, Sorci, Smith, & de Lope, 2002; McGraw & Hill, 2000b) have instead investigated within-group competitions, in which possible combinations of contestants increase exponentially with group size. However, given the frequency of interactions and the (often ignored) potential for polyadic contests, including information sharing and eavesdropping (e.g. Amy & Leboucher, 2007; Loretto, Fraser, & Bugnyar, 2012; reviewed in Sherratt & Mesterton-Gibbons, 2013), competitiveness of each individual can be more challenging to estimate in these studies.

The question then remains whether competiveness of individuals in groups/societies can be estimated from dyadic contests. In most cases, running all possible pairwise combinations of individuals through a tournament, which can clarify relative competitiveness of all group members, is unrealistic, as the number of combinations scales with $(N^2 - N)/2$; for example it would require 1225 trials in a study of 50 animals. Bayesian statistical inference may be an

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alternative solution to this problem. This approach is more accurate and informative for estimating relative competitiveness of individuals within a group, compared to classic nonparametric statistical methods such as I&SI methods (Adams, 2005; Romero & Castellanos, 2010). Moreover, Bayesian competitiveness estimates can be compared even without aggressive encounters when a series of contests takes place. In fact, based on dominant–subordinate relationships of wild male chimpanzees, *Pan troglodytes*, across two decades, Hasegawa and Kutsukake (2015) showed that competitiveness estimates could be compared across years because of the predictable link between male age and competitiveness. Likewise, in principle, a series of paired contest trials in captivity may determine the relative competitiveness of individuals within groups. This is because a series of paired contests forms a 'hypothetical competition group', which can be defined as a set of individuals for which competitiveness can be compared to the opponents, to the opponents' opponents, and so on (Fig. 1). Because previous applications of these Bayesian approaches have focused on outdoor groups, in which most of the dyadic combinations could be observed (i.e. with few blank cells in the interaction matrix; see Adams, 2005) or involved an additional predictor (i.e. age in Hasegawa & Kutsukake, 2015), the applicability of Bayesian competitiveness to a series of captive experiments remains unknown. Such an approach may also be beneficial when investigating how phenotypic variation predicts competitiveness, particularly when the focal traits are hard to manipulate experimentally (e.g. a bird's bill, other tissues containing sensory cells; Freire, Eastwood, & Joyce, 2011).

Here, we used Bayesian inference to study the relative competitiveness of male house finches, *Haemorhous mexicanus*, in captivity. This is a suitable study system, as there are no strong winner/loser carryover effects (Hasegawa, Ligon, Giraudeau, Watanabe, & McGraw, 2014; Hsu, Earley, & Wolf, 2006) and trial order should thus rarely affect contest outcome. Using the data of Hasegawa et al. (2014), we studied whether aggressive outcomes from paired contests can be used to estimate individual competitiveness across cages based on the hypothetical competition groups. Because our experiments were conducted over a relatively short period of time (ca. 7-day interval), temporal changes in male competitiveness should be minimal.

Given the competitiveness estimates from a set of pairwise trials, we tested whether and how well the estimates predicted outcomes of future contests among unfamiliar individuals within groups. Using colourful and drab males captured from urban and rural habitats, Hasegawa et al. (2014) conducted two dyadic contest experiments, a 'within-site experiment', in which we compared aggression between colourful and drab males from the same habitat type, and a 'between-site experiment', in which we staged agonistic encounters between urban and rural males that were matched for colour type, and one within-group contest experiment (a 'group competition experiment') in which we studied the relative aggressiveness of all four groups of birds (urban colourful, urban drab, rural colourful, and rural drab) by putting them into the same cage simultaneously. We used the first two experiments to estimate competitiveness of individual birds and then investigated whether the estimate differed between

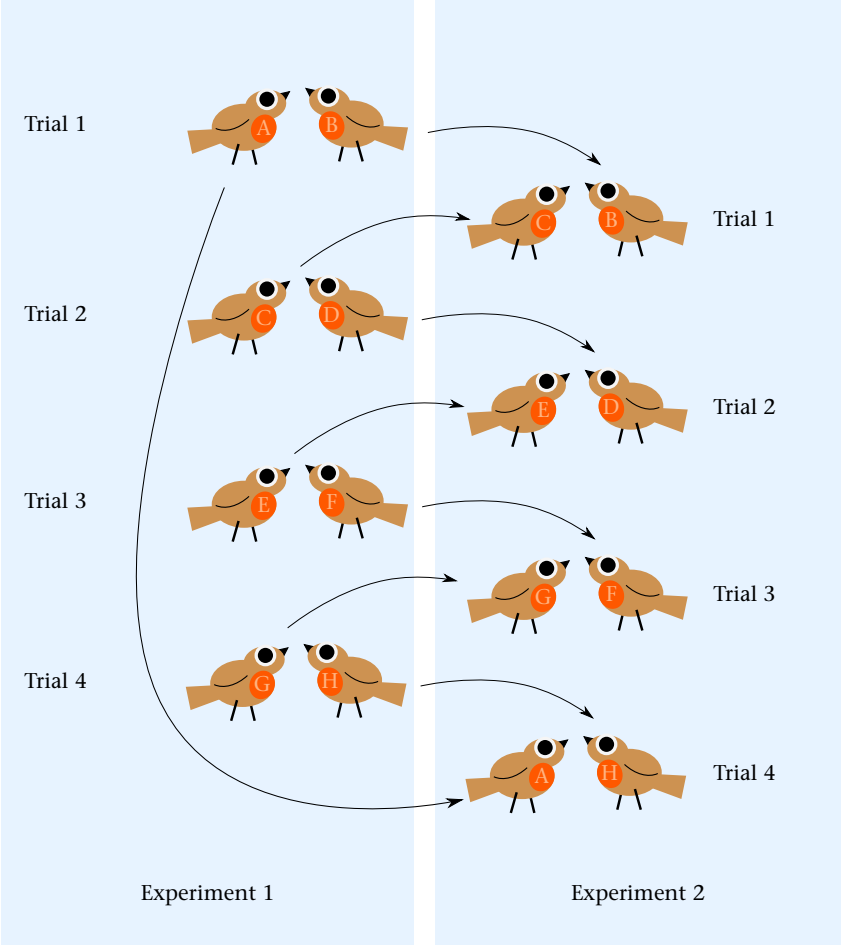

Figure 1. Competitiveness can be estimated within a 'hypothetical competition group', in which each individual competes against two different individuals, at least in principle. The same individuals are indicated by shared letters and arrows.