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Formation of linear dominance relationship in captive jungle crows (*Corvus macrorhynchos*): Implications for individual recognition

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Abstract

Jungle crows (*Corvus macrorhynchos*) flexibly change their social forms depending on their age, time of the day, and the season. In the daytime, paired adults behave territorially and unpaired subadults form small flocks of ten birds, whereas at night hundreds of birds roost together. In the breeding season, pairings remain in their nest all day. This fission–fusion raises questions about the underlying social structure and the cognitive capability of jungle crows. In this study, dyadic encounters were used to investigate dominance relationships (linear or non-linear) and the underlying mechanisms in captive jungle crows. Fourteen crows were tested in 455 encounters (*i.e.*, 5 encounters per dyad), and a stable linear dominance relationship emerged. Sex and aggressiveness were determinants as individual characteristics for dominance formation. Males dominated females, and more aggressive individuals dominated less aggressive ones. Aggressive interactions in dyads occurred primarily during the first encounter and drastically declined during subsequent encounters without any signs of a confidence effect. These results suggest that, in captive jungle crow, a linear form of dominance is intrinsically determined by sex and aggressiveness and maintained extrinsically by memories of past outcomes associated with specific individuals, implying individual recognition.

Keywords: Corvid; Crow; Dominance; Social relationship; Social cognition

1. Introduction

Animals living in groups often establish dominance relationships that produce consistent outcomes for a dyad in successive contests (Drews, 1993). A dominance relationship, once established, benefits both individuals in the dyad by reducing the cost and risk of future conflicts that may otherwise escalate (Huntingford and Turner, 1987; Clutton-Brock and Paker, 1995). Forms of dominance relationships between dyads in a group are classified as linear or non-linear according to their structures. In the linear form, dominance relationships for all possible component triads are transitive, meaning that if A dominates B and B dominates C, then A also dominates C. On the other hand, a non-linear social structure contains intransitive triads, with circular dominance links (*i.e.*, A dominates B, B dominates C, and C dominates A). In both natural and laboratory settings, linear dominance relationships have been documented in a broad range of taxa, including insects (Dugatkin et al., 1994), crustaceans (Sastry and Ehinger, 1980; Goessmann et al., 2000), fishes (Nelissen, 1985; Beacham and Newman, 1987), birds (Malar, 1955; Banks, 1956; Tamm, 1977; Heinrich, 1988), and mammals, including both non-human and human primates (Smuts et al., 1987; Savin-Williams, 1977).

Two potential mechanisms, intrinsic and/or extrinsic, have been studied to underlie the formation and maintenance of a linear dominance relationship. The first is an intrinsic mechanism in which dominance relationship is determined by individual characteristics (*e.g.* body size, age, or sex) signalling the potential dominance ability or resource holding power (RHP) of an individual (Landau, 1951a). When this mechanism is effective, a strong correlation can be expected between win/loss outcomes and the characteristics. The evolutional stability of an intrinsic mechanism and its ability to account for a linear dominance relationship has been debated (Landau, 1951a; Maynard and Smith, 1974). However, many studies indeed support a role for intrinsic mechanisms in this regard (Richner, 1989; Piper, 1997).

The second is an extrinsic mechanism in which the dominance relationship is generated through agonistic interactions and maintained based on the memory of the outcomes of past encounters (Landau, 1951b). If this second hypothesis is

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effective in a group, we can expect that during the dynamic process of dominance formation, individuals could be highly aggressive to one another in their first encounter and decrease their aggressiveness in subsequent encounters (Guhl, 1968; Goessmann et al., 2000). Dominance is not predetermined by individual characteristics; rather, it is determined *a posteriori* by the outcomes of previous encounters.

The memory basis hypothesis contains two alternate mechanisms involving memory: the so-called "confidence effect" (the winner/loser effect) and "individual recognition." The confidence effect considers that the behaviour of an individual is solely based on the outcomes of previous encounters, independent of the opponent. That is, contestants become more aggressive if they win in previous encounters and more submissive if they lose, regardless of the opponent (Barnard and Burk, 1979). Simulation studies and modelling suggest that the confidence effect can explain a linear dominance relationship (Landau, 1951b; Dugatkin, 1997; Dugatkin and Earley, 2004) and have also suggested that this effect may enhance the formation of a linear structure (Francis, 1987; Drummond and Osorno, 1992; Chase et al., 1994). Individual recognition, on the other hand, considers that an individual becomes discriminatively aggressive or submissive towards a specific opponent based on its memory of prior encounters with it. A simulation study suggests that individual recognition can be more effective than the confidence effect for the forming and maintaining a linear dominance hierarchy in a group where the frequency of successively encountering a familiar member is higher than that of encountering an unfamiliar member (Pagel and Dawkins, 1997). The involvement of individual recognition in the formation and maintenance of dominance relationships has been documented in a variety of studies (Karavanich and Atema, 1998; López and Martín, 2001; Gherardi and Atema, 2005).

Corvid species, such as crows, jays, and magpies, form complex fission–fusion societies (Emery, 2006). In this type of society, individuals strictly depend on social relationships with other group members in order to survive and solve problems. This situation is assumed to have shaped the evolution of highly intelligent behaviours in this taxon, in a way comparable to those of primates (Emery and Clayton, 2004; Emery, 2006). These behaviours include the complex form of memory (scrub jays, *Aphelocoma coerulescens*; Dally et al., 2006), prospective cache protection based on the exploitation of the individual's own pilfering experience (*e.g.*, scrub jays; Emery and Clayton, 2001), active diversion of a rival away from a food resource (*e.g.*, common ravens, *Corvus corax*; Bugnyar and Kotrschal, 2004), or inference of dominance ranks with unfamiliar individuals based on their dominance relationships with familiar jays (*e.g.*, pinyon jays, *Gymnorhinus cyanocephalus*; Paz-y-Miño et al., 2004). These studies suggest an ability of Corvid species for individual recognition in a variety of social contexts. How individual recognition plays a role in the formation of social structure has yet to be described, however.

Like other corvids, jungle crows form fission–fusion societies, with flexible change in the social structure depending on the time of day, seasons, and their age (Kuroda, 1990; Kawauchi and Matsuda, 1999a,b). During daytime, paired adults defend a territory, whereas un-paired subadults form flocks of 10 birds at periphery of territories. On the other hand, during the night and outside of the breeding season, both adults and subadults roost in large flocks of up to several hundreds of birds. During the breeding season, adults spend the night in their territory (*e.g.*, Karasawa, 2003). Although jungle crows are basically non-colonial birds, certain dominance relationships could emerge as a consequence of repeated encounters between the same individuals in a variety of settings, including feeding sites, bathing site, within subadult flocks, and in communal roosts. However, the social structure of jungle crows and the mechanisms underlying their dominance relationships remain unknown. To elucidate the social structure and mechanisms underlying its formation and maintenance, we have addressed three questions:

(1) Is dominance relationships between jungle crows linear or non-linear?
(2) Is an individual's dominance relation influenced by intrinsic or extrinsic factors?
If the extrinsic mechanisms is in effect,
(3) Which does the confidence effect or individual recognition contribute to dominance formation and/or its maintenance?

To answer these questions, we measured relative dominance relationships using dyadic encounters and analyzed whether individual characteristics and successive encounters contribute to dominance formation and/or maintenance.

2. Materials and methods

Care and use of the animals adhered to The Guideline for Experimental Animals of Keio University.

2.1. Subjects

The subjects were 14 hand-raised jungle crows. We used eight females and six males (sex determined by DNA analysis), between 2 and 10 years of age at the start of the experiment (see Table 1 for details). No crows were pair bonded. In order to prevent subjects from establishing dominance relationships by means of direct interactions outside of the experiment, crows were individually housed in stainless-steel mesh cages (W43 cm × L60 cm × H50 cm), separated from one another by 15 cm, in a three-story rack. We randomly shuffled the positions of the individual cages in the rack to allow all of the crows to familiarize with each other. Crows could see and hear each other but had no physical contact while in their cages. To generate motivation for food during the encounters, subjects were daily fed a limited amount of their normal diet of dog food and supplements, such as cheese and raisins. Thus, during the experimental period, the average body weight of each individual was 90–95% to the mean *ad libitum* body weight (defined as the mean value measured during a 2-month free-feeding period prior to the experiment; see Table 1). Water was freely available in their home cages. Subject were allowed regular access to a relatively large aviary (W1.6 m × L1.2 m × H1.7 m) to reduce the stress due to spatial constrain.