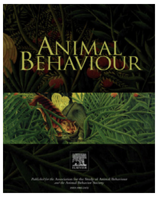
Animal Behaviour 102 (2015) 259–266

Contents lists available at ScienceDirect

Animal Behaviour

journal homepage: www.elsevier.com/locate/anbehav



Advertised quality and resource value affect aggression and social vigilance in paper wasp contests

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ARTICLE INFO

Article history:
Received 9 October 2014
Initial acceptance 12 November 2014
Final acceptance 18 December 2014
Published online
MS. number: A14-00803

Keywords:
aggression
Polistes dominula
resource value
resource-holding potential
social vigilance

Animals frequently compete over limited resources such as food, territories or mating opportunities. Contest behaviour varies based on factors such as the value of the contested resources and the agonistic ability of rivals. Much work on animal contests has examined aggression, but vigilance, or a state of heightened alertness directed towards specific stimuli, may also be an important component of competition in many species. In this study, we measure the relationships among social vigilance, aggression, agonistic ability and resource value during staged contests over nest ownership in *Polistes dominula* nest-founding wasps. Our results show that both social vigilance and aggression are involved in mediating social risk during contests. Nest owner vigilance towards a rival increased with the time of season, a measure of nest value. Owner vigilance was also positively associated with aggression such that more aggressive owners were more vigilant. During contests, aggression of owners and rivals was influenced by different factors. Owner aggression was positively associated with nest size, another measure of nest value, while rival aggression was unrelated to nest size. Instead, rival aggression was associated with facial patterns that function as signals of agonistic ability; rivals were less aggressive to owners that signalled high agonistic ability than they were to owners that signalled low agonistic ability. The distinct predictors of contest behaviour between owners and rivals indicate that competitive role has a surprisingly strong influence on cues used to inform contest behaviour. Differences may occur because owners and rivals have different information and/or motivation. These results also suggest that social vigilance and aggression may be complementary behaviours that animals use to mitigate social threat.

Animals frequently compete over limited resources such as food, territories or mating opportunities. Aggressive competition is costly; so many animals have evolved strategies to maximize the benefits they receive relative to the costs of competition (Maynard Smith, 1974). As a result, the likelihood of engaging in contests and contest behaviours displayed vary based on factors such as the value of the contested resources (Lindström, 1992) and agonistic ability of rivals, also known as resource-holding potential (Hunt, Bennett, Cuthill, & Griffiths, 1998; reviewed in Arnott & Elwood, 2009).

Theoretical and empirical work has shown that resource value and resource-holding potential influence the length and intensity of animal contests (Maynard Smith & Parker, 1976). Typically, contests over more valuable resources are longer and more intense than contests over less valuable resources (Enquist & Leimar, 1987). Also, in many species, factors such as body mass (Pavey & Fielder, 1996), condition (Rémy, Grégoire, Perret, & Doutrelant, 2010) and weapon size (Sneddon, Huntingford, & Taylor, 1997) are linked with individual resource-holding potential and influence both willingness to engage in contests and behaviour during contests. In taxa with conventional signals of agonistic ability, signal elaboration is used to assess rival resource-holding potential more directly; signal elaboration affects the likelihood of engaging in competition and contest behaviour (Searcy & Nowicki, 2005; Senar & Camerino, 1998).

Much of the work on animal contests has examined aggression during contests, but rival interactions are not limited to aggression (Bednekoff & Lima, 1998). Animals may use other behaviours such as grouping (Pappano, Snyder-Mackler, Bergman, & Beehner, 2012) and vigilance, or a state of heightened alertness directed towards specific stimuli, during situations with the potential for conflict (Treves, 2000). There is extensive evidence that vigilance is an antipredation tactic that is influenced by predation risk (Lendrem,

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http://dx.doi.org/10.1016/j.anbehav.2015.01.031
0003-3472/

1983), group size (Mooring, Fitzpatrick, Nishihira, & Reisig, 2004), position within a group (Keys & Dugatkin, 1990) and habitat structure (Griesser & Nystrand, 2009).

Vigilance may also be used to modulate social risk, acting as a first line of defence when there is potential for social conflict (Kutsukake, 2006). This type of vigilance, hereafter referred to as 'social vigilance', differs from vigilance directed towards predators as the context and motivating factors vary (i.e. avoid predation versus mitigate within-group conflict). Social vigilance is likely an important factor influencing the dynamics of group-living organisms. For example, individuals may direct more visual attention to dominant individuals within groups, or to unfamiliar individuals (high potential for social conflict) than to subordinates or familiar individuals (lower potential for social conflict) (Kutsukake, 2006). Social vigilance is sometimes called social monitoring and is known to occur in a range of primates, where social information is important because of complex group structure and long-term interaction (Treves, 2000; common squirrel monkeys, *Saimiri sciureus*: Caine & Marra, 1988; capuchin monkeys, *Cebus apella*: Hirsch, 2002; chimpanzees, *Pan troglodytes*: Kutsukake, 2007; blue monkeys, *Cercopithecus mitis*: Gaynor & Cords, 2012). Social vigilance has also received attention in some nonprimate vertebrates (European rabbits, *Oryctolagus cuniculus*: Roberts, 1988; northwestern crows, *Corvus caurinus*: Robinette & Ha, 2001; wading birds (*Vanellus vanellus*, *Calidras alpine*, *Himantopus himantopus*): Barbosa, 2002; giraffes, *Giraffa camelopardalis*: Cameron & du Toit, 2005; eastern grey kangaroos, *Macropus giganteus*: Favreau, Goldizen, & Pays, 2010).

Most previous work on social vigilance comes from observational studies of stable social groups, which impose limits on the type of information that can be obtained (Cameron & du Toit, 2005; Favreau et al., 2010; Robinette & Ha, 2001). In particular, it can be challenging to tease apart exactly which factors cause variation in vigilance (Bednekoff & Lima, 1998; Hirsch, 2002). For example, it is often difficult to distinguish between social vigilance and predation-related vigilance in field studies (Hirsch, 2002). In addition, agonistic contests are common in many species, but can be difficult to observe in the field (Rubenstein & Shen, 2009). As a result, little is known about the role of social vigilance during agonistic competition.

Although aggression and social vigilance are both forms of investment in social competition, the interactions between these two behaviours remain unclear. Aggression and social vigilance could be complementary such that similar factors influence both (e.g. a nearby conspecific elicits both vigilance behaviour and aggression; Knight & Knight, 1986). Alternatively, aggression and social vigilance could be independent, with investment in vigilance occurring in some contexts (i.e. nearby conspecific) and investment in aggression occurring in other contexts (i.e. conspecific performing a threat display). The specific scenarios in which animals display social vigilance versus aggression may depend on their differing suites of costs and benefits. Vigilance is typically thought to be less costly than aggression, as there is no risk of injury (Dukas & Clark, 1995). Vigilance is not cost-free, however, as it imposes time costs; time spent being vigilant reduces time devoted to other activities such as foraging, resting or parental care (Toïgo, 1999). The benefits of social vigilance versus aggression also differ, as aggression is well known to deter rivals, while there is little evidence that vigilance alone acts as a deterrent (Caine & Marra, 1988).

In this study we measure the relationships among social vigilance, aggression, resource-holding potential and resource value during contests over nest ownership in *Polistes dominula* (paper wasp) nest-founding queens. *Polistes dominula* provide an excellent system to study the dynamics of intraspecific competition, as conflict over nest ownership is widespread in *Polistes* (Field, 1992). Nest usurpation is common, during which a new queen takes over an established nest and rears the resident larvae and pupae, thus ensuring a future workforce to care for her own offspring (Starks, 2001). Nest usurpation is an important selective force in paper wasps because of its direct impact on reproductive success as well as the intensely aggressive, and even fatal, nature of usurpation battles (Gamboa, 1978). Therefore, we tested the question: do *P. dominula* nest owners display social vigilance, in addition to aggression, as a defensive behaviour during competition over nest ownership?

Polistes dominula also provide a good system to test how resource value and resource-holding potential influence contest behaviour, as both resource value and resource-holding potential are straightforward to measure. Two measures of resource value were used in this study: nest size and time of season. The nest size (i.e. number of cells) provides a good measure of resource value; when choosing between adopting larger versus smaller nests, *P. dominula* wasps significantly prefer larger nests (Nonacs & Reeve, 1993), perhaps because larger nests facilitate greater reproductive output. The time of season is also associated with resource value in *P. dominula*, as later-season nests are more valuable than early-season nests (i.e. larger comb size and greater brood maturity; Nonacs & Reeve, 1993). Furthermore, if a wasp's nest is usurped late in the season, there is insufficient time for her to build a new, successful nest (Downing & Jeanne, 1988). In *P. dominula*, nests are started relatively synchronously (Gamboa, Greig, & Thom, 2002).

Two measures of individual resource-holding potential were used in this study: body size and facial pattern. Body size is often associated with fighting ability in *Polistes* (Turillazzi & Pardi, 1977; but see Zanette & Field, 2011; reviewed in Jandt, Tibbetts, & Toth, 2014). Facial patterns also function as condition-dependent signals of fighting ability in *P. dominula* (Tibbetts, 2010; Tibbetts & Lindsay, 2008). *Polistes dominula* individuals with more broken black facial patterns are more likely to win fights than those with less broken black facial patterns (Tibbetts & Dale, 2004), and wasps use facial patterns to assess rivals prior to engaging in social interactions (Tibbetts & Lindsay, 2008). *Polistes dominula* facial patterns are also linked with traits related to agonistic ability including juvenile hormone titre (Tibbetts, Izzo, & Huang, 2011) and nutrition during early development (i.e. body size; Tibbetts, 2010). In *P. dominula*, there is geographical variation in facial patterns. Some European populations have very low facial pattern variation, as most individuals have entirely yellow facial patterns associated with low agonistic ability (Cervo, Dapporto, Beani, Strassmann, & Turillazzi, 2008; Tibbetts, Skaldino, et al., 2011). In populations with low facial pattern variation, facial patterns may not function as signals of resource-holding potential (Green & Field, 2011; Zanette & Field, 2011). However, there is ample evidence that facial patterns signal resource-holding potential in the population of *P. dominula* used in this study (reviewed in Tibbetts, 2013).

In this study, we test the relationships between aggression, social vigilance, resource value and resource-holding potential. We hypothesized that vigilance and aggression of nest owners would be positively associated. Furthermore, we predicted that wasps would be more aggressive and vigilant when competing over high-value nests than when competing over low-value nests. Finally, we predicted that resource-holding potential would be related to aggression such that individuals would be less aggressive towards rivals with high resource-holding potential, as compared to those with low resource-holding potential.

METHODS

Wasp Collections

Single foundresses and their nests were collected from sites around Ann Arbor, MI, U.S.A. in May and June 2011 from 0600 to