



Understanding intrinsic and extrinsic drivers of aggressive behaviour in waterbird assemblages: a meta-analysis



Kevin A. Wood^{a, *}, Jessica Ponting^a, Nathan D'Costa^a, Julia L. Newth^a, Paul E. Rose^{a, b}, Peter Glazov^c, Eileen C. Rees^a

^a Wildfowl & Wetlands Trust, Slimbridge, Gloucestershire, U.K.

^b Centre for Research in Animal Behaviour, College of Life & Environmental Sciences, Washington Singer, University of Exeter, Exeter, U.K.

^c Institute of Geography, Russian Academy of Sciences, Moscow, Russia

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Aggressive behavioural interactions between animals are widespread in nature, with ecological and evolutionary consequences of such interactions reported for both individuals giving and receiving aggression. Yet despite the importance of aggressive interactions in determining social dominance and conferring fitness benefits to successful individuals, we lack a general understanding of the conditions that influence the variation in agonistic behaviours among individuals and species. We conducted a global meta-analysis of published time–activity budgets, using a data set comprising 555 values from 88 studies, to determine variation in the time that waterbirds engaged in aggressive interactions. The mean \pm SD percentage of time devoted to aggression was $2.0 \pm 3.6\%$, with a range of 0.0–35.0%. We used our data set to test four predictions regarding avian aggression, based on the findings of earlier site-based studies. We predicted that the time spent on aggression would be influenced by four factors: (1) age class, (2) sex, (3) seasonal timing and (4) functional feeding group. A comparison of linear mixed-effects models using an information theoretic approach indicated that the proportion of time waterbirds spent engaged in aggressive interactions was best explained by the age class and sex of the focal waterbird species. More time was spent on aggression by males than females, and by adults than juveniles. We found no evidence that the time spent on aggressive behaviours varied across latitudes or body mass, with seasonal timing, sexual dimorphism, migration or breeding strategies, or between different functional feeding groups. Our findings highlight the high levels of variation in the time devoted to aggression across species, feeding groups, latitudes and seasons. Furthermore, our study demonstrates the utility of the numerous published time–activity budget studies that are available as a valuable source of data that can be used to answer broad-scale questions regarding animal behaviour.

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Aggressive behavioural interactions between individuals of the same or different species are a widespread phenomenon in nature and have been reported for a wide range of animal taxa, from molluscs to mammals (Huntingford & Turner, 1987; King, 1973; Peiman & Robinson, 2010). Such behavioural interactions range from threat displays aimed at opponents to direct physical attacks (Archer, 1988; Collias, 1944). Decades of research have revealed that there is no one single underlying cause of aggression between individuals, although key triggers include competition for limiting resources such as food or nest sites, defence of such resources from

conspecifics and heterospecifics, and defence against predators or intruders (Archer, 1988). Aggressive behaviours allow animals to compete with other individuals for, and potentially exclude other individuals from, valuable resources such as food and breeding sites (Peiman & Robinson, 2010; Pelligrini, 2008). Similarly, aggression can also be used to steal resources from either conspecifics or heterospecifics, for example through kleptoparasitism (Amat, 1990; Brockman & Barnard, 1979; Holm & Clausen, 2009; Waltho, 2009; Wood, Stillman, & Goss-Custard, 2015). Aggressive behaviours are also used to defend the aggressors' offspring from predators and feeding competitors (Kontianen et al., 2009; Larsen, Sordahl, & Byrkjedal, 1996).

A growing body of research has highlighted the important ecological and evolutionary consequences of aggressive interactions between both conspecifics and heterospecifics, for both

* Correspondence: K. A. Wood, Wildfowl & Wetlands Trust, Slimbridge, Gloucestershire GL2 7BT, U.K.

E-mail address: kevin.wood@wwt.org.uk (K. A. Wood).

individuals giving and receiving aggression (Grether et al., 2013; Murray, 1971). Aggressive behaviours influence individual rates of resource acquisition, growth rate and body condition, typically with positive effects for the aggressor and negative effects for the individual receiving aggression (Amat & Obeso, 1991; Black & Owen, 1989; Peiman & Robinson, 2010). However, there are costs to the aggressor in terms of greater energy expenditure, lost foraging time, and increased risks of injury and death (Jaeger, 1981; Marler & Moore, 1989). Therefore, observed levels of aggression will reflect a trade-off between the potential gains and costs (Archer, 1988). The ability to secure resources such as a breeding site and adequate food resources through aggression can benefit reproductive success and fitness (Peiman & Robinson, 2010). Aggression can have implications not only for individual fitness but also for recruitment to the population; for example, Kontiainen et al. (2009) found that female Ural owls, *Strix uralensis*, that displayed greater aggression during the defence of their nests produced more fledged young. More widely, a meta-analysis of the fitness consequences of animal personality traits by Smith and Blumstein (2008) found that aggressiveness had a positive effect on reproductive success. The magnitude of intraspecific and interspecific competition for resources within a landscape will at least partly determine the carrying capacity of an environment and hence population sizes (López-Sepulcre & Kokko, 2005).

Time–activity budgets are an approach used to quantify how individuals apportion time for different behavioural activities (Paulus, 1988). The compilation of time–activity budgets from behavioural observations of animals is a common approach used to quantify the time spent in aggressive interactions (Altmann, 1974; Paulus, 1988). Individually, time–activity budget studies are limited in their number of focal individuals and species, as well as in their spatial and temporal extent. Consequently, we currently lack a comprehensive understanding of the intrinsic and extrinsic factors that influence the strength of aggressive interactions between individuals within populations. However, the availability of numerous time–activity budget studies using similar methodologies enables a meta-analysis approach to be used to draw more general conclusions (e.g. Cotgreave & Clayton, 1994). For effective meta-analysis, researchers need to achieve adequate sample size and data range in the variables of interest, and yet limit the number of confounding variables by using appropriate selection criteria for inclusion of studies in the meta-analysis (Gates, 2002). Over the last 50 years, numerous time–activity budget studies have been carried out on aggression among waterbirds (Paulus, 1988), and so the use of waterbirds as a focal taxon allowed us to maximize data availability for our analysis. Among waterbirds, aggression towards other individuals is based on observable physical behaviours which consist of pecks with the beak, trampling with the feet and body, and strikes with the wings (Johnsgard, 1965). In contrast, certain other bird taxa (e.g. Passerines) may use vocalizations or chemical secretions rather than physical displays in aggressive interactions (e.g. Hagelin & Jones, 2007; Searcy, Anderson, & Nowicki, 2006). These nonphysical means of aggression would not be detected by a time–activity budget study, and so attempts to compare levels of aggression across all avian taxa could be confounded by variation in the modes of aggression used by different groups.

Herein, we tested four predictions related to the time devoted to aggressive interactions, and the influence of intrinsic and extrinsic factors. Our predictions were informed by the results of previous studies which had identified key variables that influenced the time devoted to aggression in certain species assemblages. For many bird species, adults, especially males, devote more time to the defence of feeding areas, territories and offspring, and hence spend more time involved in aggressive interactions with conspecifics and heterospecifics (Fedy & Stutchbury, 2005; but see Côté, 2000).

Aggressive interactions may vary in time, as well as between species with different feeding characteristics (Paulus, 1988). Levels of aggression may vary seasonally due to changes in breeding status (i.e. the need to defend a nest or offspring) or feeding requirements (e.g. high levels of competition at migratory stopover sites) (Wingfield, Ball, Dufty, Hegner, & Ramenofsky, 1987). Finally, aggressive interactions linked to shared resources such as food may vary in magnitude depending on how feasible it is to acquire and defend those shared resources (Murray, 1971), and thus the levels of aggression observed may vary between groups of waterbirds with different feeding characteristics such as diet and foraging mode.

Thus, our first and second predictions were that the time devoted to aggressive interactions would vary with age class and sex, such that greater proportions of time would be spent on aggressive behaviours by adults than juveniles, and by males than females. Finally, our third and fourth predictions were that the time devoted to aggressive interactions would vary with seasonal timing (with greatest levels of aggression during the breeding season), and feeding group (with greatest levels of aggression associated with geese and swans), respectively.

METHODS

Literature Search, Inclusion Criteria and Data Extraction

Our meta-analysis was restricted to time–activity budget studies of waterbirds, which we defined as species that live on or around aquatic habitats (sensu Boere, Galbraith, & Stroud, 2007). To identify suitable studies of waterbird aggression for our meta-analysis we carried out literature searches using Google Scholar, which were completed on 30 April 2016. In Google Scholar, we searched using all combinations of one waterbird search term ('waterbird', 'waterfowl', 'wildfowl') together with one behavioural search term ('aggression', 'aggressive', 'interspecific', 'behavior', 'behaviour', 'interaction') with the Boolean operator 'AND'. Additionally, we searched previously published reviews and meta-analyses of aggressive interactions among birds and waterbird behaviour for suitable primary studies (Kear, 2005; King, 1973; Murray, 1971; Paulus, 1988; Taylor, 1998).

The search results were manually screened for suitability for inclusion in our meta-analysis; each study was required to contain sufficient information to calculate the percentage of time devoted to aggressive behaviours from a time–activity budget, along with the full range of explanatory variables. Thus, we required studies to present the relative time devoted to aggression or agonistic behaviours (where agonism represented only aggressive interactions). Studies that did not present data on aggression separately from other behavioural categories (e.g. combined with one or more other behaviours such as vigilance or courtship behaviours) were discarded from our analysis. Time–activity budget studies report field observations rather than treatment–control contrasts, and so it was not possible to calculate an effect size as is typically done in a meta-analysis study (Koricheva, Gurevitch, & Mengersen, 2013). Furthermore, many original studies did not report any measure of variance associated with the time the focal population spent on aggression. Therefore, our analysis was based on the values of time devoted to aggression reported in each of the original studies.

We further limited our analysis to those studies for which the following explanatory variables were reported (or available elsewhere in the published literature): focal species name, sex and age class of the focal individuals, seasonal timing of the study, the latitude of the study system, mean body mass of the focal species, migratory strategy (sedentary or migratory) of the focal species,

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