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Aggressive interactions in Swan Geese *Anser cygnoides* and their hybrids

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Abstract. Evidence for direct interspecific competition in wildfowl and between hybrids and their parent species is scarce. This study examined threat displays and agonistic encounters (n = 324) in a goose flock of 140 Swan Geese and 13 hybrids with Greylag Goose living in Heidelberg, SW Germany. In general, agonistic behaviour made up less than 1% of the time budget throughout the year as measured by focal animal sampling. Most encounters (84%) were won by the initiator, both in Swan Geese and in hybrids. No difference was found between Swan Geese and hybrids in the outcome of an encounter, suggesting equal competitive quality. There were differences with respect to threat postures with hybrids performing diagonal neck threats more often and intentional movements less often. This seems to be related to their hybrid origin, since Greylag Geese most often show diagonal neck and forward threat displays. There was no direct evidence for hybrid superiority or inferiority.

Key words: Swan Goose, *Anser cygnoides*, Greylag Goose, *Anser anser*, aggressive behaviour, foraging, hybrid superiority, competition, threat postures, wildfowl

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INTRODUCTION

Different aspects have to be considered when investigating aggressive behaviour within a goose flock and between a true species and its hybrids. While feeding in a flock, most birds maintain an individual distance by threatening, attacking or fleeing from other approaching individuals (Hinde 1973). Usually, geese are feeding during a large part of the day. According to optimal foraging theory (Krebs & Davies 1996) geese should reduce costs of locomotion by avoiding interference and interactions with conspecifics. These interactions are costly compared to other behaviour, e.g. in Barnacle Geese *Branta leucopsis* they reach 2.3× of their basal metabolic rate compared to 1.5× when resting or 1.6× when foraging (Stahl et al. 2001c). As a consequence the reduction of costly interactions permits the most efficient use of resources (Stahl et al. 2001b) because avoidance of direct interactions with neighbours pays in terms of foraging time and avoidance of costs of locomotion.

Many studies investigating time budgets of foraging waterfowl reveal a low proportion of time spent in aggressive encounters and interactions (usually below 1%; Paulus 1988, Baldassarre & Bolen 1994, Mathers & Montgomery 1996, Nyegaard et al. 2001), although studies carried out using flock scan methods often underestimated behaviour that rarely occurs (Baldassarre et al. 1988). Studies using focal animal samplings instead (e.g. Pietz & Buhl 1999) confirm a low proportion of time spent in interactions. For example, Stahl et al. (2001a) recorded 27 interactions during 267 minutes of focal observations of Barnacle Geese. Würdinger (1978) found a basic proportion of 5.6% of time spent in encounters in Bar-headed Geese *Anser indicus* under semi-natural conditions. Black & Owen (1988) classified interactions according to energetic requirements in Barnacle Geese and found that the percentage of agonistic types decreased as the physical demands increased, which is also in correspondence with the assumption of cost reduction.

Intraspecific aggression may be affected by several interrelated factors, e.g. food abundance or nesting density, while interspecific interactions may depend additionally on factors like body size or breeding system (Garcia & Arroyo 2002). For example, larger individuals won more interactions, and adult birds were dominant over first winter birds in Purple Sandpipers *Calidris maritima* (Burton & Evans 2001); age played an important role in dominance relationships of geese (Stahl et al. 2001b) as subordinates were forced to forage on patches of minor food quality. Aggression and dominance differed between subspecies, e.g. in Juncos *Junco* sp. (Wiedenmann & Rabenold 1987) or even in different populations of Blue Tits *Parus caeruleus* from the same island (Braillet et al. 2002). However, most aggressive interactions in waterfowl are intraspecific and occur while one or both participants are feeding (Baldassarre & Bolen 1994). Interspecific conflicts in geese species have been described by Frazer & Kirkpatrick (1979) who showed that Cackling Canada Geese *Branta canadensis minima* always retreated when confronted with a family of Emperor Geese *Anser canagicus*. Owen & Black (1990) concluded that interspecific competition might not directly lead to conflicts but the smaller species might be outplaced towards less profitable areas. Madsen & Mortensen (1987) neither found evidence for active interspecific aggression between Pink-footed Geese *Anser brachyrhynchus* and White-fronted Geese *Anser albifrons* but assumed that the poor competitor may occupy alternative sites or sub-optimal habitats. Kristiansen & Jarret (2002) observed 48 encounters between Greenland White-fronted Geese *Anser albifrons flavirostris* and Canada Geese *B. c. interior* and found all the encounters to be won by Canada Geese.

Hybrid superiority has been described in some plant species (Arnold & Hodges 1995). Well-known examples in animals are the hybrid vigour of the mule (Short 1975) and of some crosses in mice (Moulia et al. 1995), while studies dealing with birds usually report no hybrid vigour or superiority (exceptions of bounded hybrid superiority, e.g. Grant & Grant 1996, Good et al. 2000). In studies using mounted specimen, Pearson & Rowher (2000) found Townsend's Warbler *Dendroica townsendii* and their hybrids with Hermit Warbler *D. occidentalis* competitively superior to Hermit warblers. In wildfowl, Black Duck *Anas rubripes* x Mallard *Anas platyrhynchos* hybrids showed higher salt tolerance than Mallards and were more similar to Black Ducks in this respect (Barnes & Nudds 1991), but in contrast, parasite load was higher in hybrids compared to both parent species (Mason & Clark 1990), therefore, hybrid vigour in wildfowl does not seem to be a general phenomenon.

Interactions and encounters between hybrids and true wildfowl species are difficult to study and interpretation of available data is often hampered by low sample sizes. To date, only some anecdotal evidence are published (e.g. Randler 2002, 2003a, but see Brodsky & Weatherhead 1996).

This study aims at describing and comparing the organisation of a goose flock with regard to agonistic behaviour of both Swan Geese and their hybrids. Another aim is to investigate hybrid superiority or inferiority, measured with respect to the outcome of encounters and, further, to compare threat postures between hybrids and Swan Geese.

STUDY AREA AND SPECIES

The Asian Swan Goose is endangered throughout its entire range (Birdlife International 2001) and breeds mainly in Siberia and China (del Hoyo et al. 1992). Swan Geese and their domestic forms (Grey African, Grey Chinese) are non-native species to Europe. Swan Geese were first reared in captivity in China 3000 years ago and were introduced to Europe in the eighteenth century (Delacour 1954–1964). The resident flock in Heidelberg in southwest Germany (8°41'E, 49°25'W) is among few flocks with regular reproductive success in Europe (Delany 1993, Hagemeijer & Blair 1997). The founders of this flock have bred in single pairs at least since the mid 1990s, e.g. eight pairs in 1996 and seven in 1997. The habitat consists of a public lawn, which stretches over 1.1 km along the river Neckar with a maximum width of 60 m totalling an area of 5.5 ha in size. Breeding took place on a small island within the river Neckar. Although not permitted, public feeding was commonplace. Most individuals resembled Swan Geese or domestic breeds (n = 140), but at least 13 individuals were F_1-hybrids with Greylag Goose or F_2-hybrids and backcrosses. Hybrids between these two species are common in waterfowl collections and among animals that are bred for use by humans either as egg or meat producers (Lühmann 1953, Delacour 1954–1964, Gray 1958, see Meyer 1995 for a backcross) and have already been described by Darwin (1859). Identification of such hybrids is straightforward because of their characteristic leg and bill colour, hind neck

coloration, eyering and pale forewing: forehead, crown, nape and hind-neck are dark brown and contrasting with paler cheeks and ear coverts; the bill resembles Swan Goose in size and structure, but is yellowish with some black markings; there is a slight yellowish eyering; the forewing is pale grey as in Greylag Goose (see photos in Randler 2001). The birds have habituated towards human disturbances (Randler 2003b).

Other waterfowl present at the study site were few Mute Swans *Cygnus olor*, one Pink-footed Goose, two Tundra Bean Geese *A. fabalis rossicus*, Mallards and Coots *Fulica atra*.

METHODS

Focal animal sampling (Martin & Bateson 1993) was carried out between 15 February 2002 and 29 January 2003, and every 15 s the behaviour was classified into different categories (feeding, resting, locomotion, comfort behaviour, vigilance, courtship behaviour and aggressive interactions). To sample agonistic encounters the following sampling technique was used (Martin & Bateson 1993): a randomly chosen group of focal birds was observed and all the contacts were recorded in which the status of the contestants could be determined (Boyd 1953). Such behavioural samplings are advantageous in recording infrequent or rare behaviour compared to flock scans or focal animal samplings (Baldassarre et al. 1988, Martin & Bateson 1993). To avoid over-sampling of a small sub-set of individuals or of groups, focal birds were randomly chosen and observation groups were changed every 10 minutes. Encounters were opportunistically sampled throughout the year, but most research was carried out on six days during December 2002 and January 2003, where sampling was especially devoted to recording encounters.

An interaction was defined as a direct confrontation between two birds, ranging from threat postures to active chases and body contacts. Usually, conflicts were resolved within seconds (compare Stahl et al. 2001b). The encounters were classified into three groups: won, lost, and draw. An individual was considered to have won an encounter when the other one left the area (walking away, running, flying). Draw was considered when the opponent displayed back at the initiator, but both stayed, or when the opponent ignored the threat. An encounter was defined as lost, when the initiator itself left the area.

Threat postures were assigned to one of the following categories: 1) the long neck stretch which is described for Bean Goose *Anser fabalis* ssp. and Bar-headed Goose (Johnsgard 1965), and generally for all *Anser* species in Owen (1980); 2) the diagonal neck display which is reported in Swan Goose (Johnsgard 1965) and Greylag Goose (Bauer & Glutz von Blotzheim 1968); 3) the forward threat display which is also reported for both species and for all other *Anser* species (Johnsgard 1965, Bauer & Glutz von Blotzheim 1968); 4) a slight movement of the head which is a posture closely resembling the bent neck (Johnsgard 1965) which was reported for White-fronted Geese *A. flavirostris* by Boyd (1953); this posture shows aggressive intent and is defined as an „intentional movement" hereafter; 5) contact meant any posture where the initiator pecked towards the opponent or showed any other physical contact (e.g. ramming). Serial contacts were defined when the opponent displayed and threatened back. These were scored as single occurrences (see Boyd 1953).

It is not known to what extent the same birds were sampled in different encounters, because the population was not ringed. Therefore, individuals may have contributed more than once to the data set (pseudo-replication, *sensu* Hurlbert 1984). I tried to account for this problem by randomly selecting focal groups and by randomly changing these groups after 10 minutes of observation so that chances of sampling the same individual during one observation bout was reduced to a minimum.

For generating the tables and carrying out the χ^2-statistics the crosstab function from SPSS 10.0 was used based on the raw data (Bühl & Zöfel 2002).

RESULTS

Analysis of encounters

Throughout the year, the percentage of aggressive behaviour was well below 1% (using the focal animal sampling technique). A total number of 357 encounters were observed, with 289 (81%) in December 2002 and January 2003. 338 encounters were directed towards Swan Geese or hybrids, one towards a dog, seven towards Carrion Crows *Corvus c. corone* and 11 towards other wildfowl. The latter 19 encounters were excluded form the analysis as were three encounters that were initiated by other wildfowl (Mute Swan, Pink-footed Goose, Tundra Bean Goose) and directed towards Swan

Table 1. Results of aggressive interactions (%) in Swan Geese and hybrids.

Result	Initiator			Receiver		
	Hybrid (N = 44)	Swan Goose (N = 280)	Total (N = 324)	Hybrid (N = 26)	Swan Goose (N = 298)	Total (N = 324)
Lost	2.3	2.5	2.5	92.3	83.5	84.2
Draw	9.0	13.9	13.3	7.7	13.8	13.3
Won	88.7	83.6	84.2	0	2.7	2.5
Overall		$\chi^2_2 = 0.79$, p = 0.67			$\chi^2_2 = 1.58$, p = 0.45	

Geese or hybrids. Only those encounters initiated by and directed towards Swan Geese or hybrids were used. Out of these remaining encounters (n = 335), all threats displayed in summer including families (n = 11) were excluded. Afterwards 324 encounters remained and were subsequently used for analysis. 280 encounters were initiated by Swan Geese and 44 by hybrids (Table 1).

Swan Geese and hybrids that induced an encounter were more likely to win than to loose or draw back. Swan Geese won 83.6% and hybrids 88.7% of the encounters they had induced. From the perspective of the receiver it was vice versa with 83.5% lost by Swan Geese and 92.3% lost by hybrids. In general, there was no significant difference in the outcome of an encounter between Swan Geese and hybrids, neither from the perspective of the initiator nor from the receiver (Table 1), suggesting an equal competitive behaviour of both.

To assess dominance relationships between both forms, these encounters were analysed separately. 36 encounters were initiated by hybrids and directed towards Swan Geese. 31 (86%) out of them were won by the hybrids. Vice versa, 16 out of 18 encounters (89%) from Swan Geese directed towards hybrids were won by Swan Geese. These results suggest that neither of these forms is competitively superior over the other in terms of direct encounters. There was no significant difference in the outcome of encounters between Swan Geese and hybrids ($\chi^2_2 = 0.51$, p = 0.78, n = 54).

Threat postures

The long neck stretch was observed in Swan Geese only once and never in hybrids (Table 2). The main threat postures reported for the grey geese *Anser* — namely diagonal neck and forward threat display with the latter being more aggressive and often preceding attacks (Johnsgard 1965) — were the most common threat postures observed in hybrids. Intentional movement (head lowered with bill pointed downwards) was the most common threat posture in Swan Geese, followed by contact.

There were significant differences in frequency of threat postures presented by Swan Geese and hybrids ($\chi^2_4 = 40.76$, p < 0.001).

Hybrids displayed diagonal neck threats more often and intentional movements less often than expected (Table 2). Physical contacts between two individuals were reported in 77 out of 324 situations (Table 2), but most of them were only brief, when bill or head of the initiator had contact with the body of the receiver.

There was no relationship between a specific threat posture and the outcome of an encounter either in Swan Geese ($\chi^2_8 = 11.28$, p = 0.19, n = 280) or in hybrids ($\chi^2_6 = 7.44$, p = 0.28, n = 44; note that one category did not occur in hybrids and therefore was omitted from the analysis; see Table 2), thus suggesting that threat postures might be adjusted to specific situations. In nine encounters initiated by Swan Geese and one by a hybrid (3%, n = 10) the birds performed a serial encounter with the opponent threatening back. Eight out of these ten cases were then won by the opponent (the former receiver) and the former initiator lost.

Table 2. Threat postures in Swan Geese and hybrids. Significances given as p < 0.001*.

Threat posture	Initiator		Total	%
	Swan Goose	Hybrid		
Long neck stretch	1	0 ns	1	0.3
Diagonal neck	36	20*	56	17.3
Forward threat	51	12 ns	63	19.4
Intention movement	125	2*	127	39.2
Contact	67	10 ns	77	23.8
Overall	$\chi^2_4 = 40.759$	p < 0.001	324	100

DISCUSSION

On the assumption that a high rate of intentional movement reduces costs, geese in my study flock seem to minimise costs of encounters. There was a low proportion of serial encounters (3%) and, generally, a low proportion of time spent in aggressive encounters as measured by focal animal sampling. Most encounters were won by the initiators. Similar results have been obtained in other studies on wildfowl (e.g. Boyd 1953, Lazarus & Inglis 1978, Baldassarre & Bolen 1994, Inglis et al. 2000). Boyd (1953) found that about 84% of the interactions in White-fronted Geese are won by the initiator. This is comes close to the amount observed in this study (84.2%, Table 1). In serial encounters, most birds that displayed back won the encounter. Threat postures (and their costs) might be adjusted to specific situations, thus suggesting that the initiator decides which posture to use to win the conflict, but takes the lowest threat intensity possible to avoid costs. An individual might initiate an aggression when there is a high probability of achieving success, and, further, less intensive forms occur more frequently as stated by Baldassarre & Bolen (1994).

Boyd (1953) registered a low amount of physical contacts between the contestants (4.4%) which differs from the present study (23.8%). In the present study, most of these physical contacts were only brief, while in other studies contacts were often preceded by running. I suppose that contacts could be less costly in my study flock because of low individual distances. The stability of the flock under these semi-natural conditions may play a role in the aggressive interactions of the flock mates. There may be a more or less stable dominance hierarchy in the flock that makes continued interactions with neighbours superfluous. The low number of interactions probably mean that individuals do not engage into yet another interaction with the flock neighbour whom they know so well that they can judge the outcome of a potential fight in advance.

Boyd (1953) reports that 16% of attacks were resisted, but the attacker was repelled only in one-third (5.3%) similar to present study (2.5%).

Although many direct aggressions between Swan Geese and hybrids were observed, they did not differ in their outcome with regard to which species attacked. Hybrids were neither inferior nor superior. Nevertheless, competition might not necessarily occur directly, but could lead to a displacement of the hybrids into less profitable areas, because they may be the poorer competitor. Such a situation was found in Pink-footed Geese (Madsen & Mortensen 1987) and in Greenland White-fronted Geese (Kristiansen & Jarrett 2002) with the latter supplying evidence for the inferiority of one species in direct competition. Kristiansen & Jarrett (2002) recorded 48 interactions between Canada Geese and Greenland White-fronted Geese which were all won by Canada Geese. In my own study I do not find evidence for competitive superiority of one form over the other. One reason might be that there is no such marked size difference between hybrids and Swan Geese as in the examples mentioned above.

The aggressive behaviour of hybrids has recently been studied in domesticated birds, such as Chicken *Gallus gallus domesticus*. These studies revealed no differences in aggressive behaviour between different strains (e.g. Kjaer et al. 2001), while in some warbler *Dendroica* species Pearson & Rohwer (2000) found hybrids to be superior over one of its parent species. My present study gives some evidence that hybrids may be of equal competitive quality as one of their parent species. Studies showing hybrids in birds to be intermediate in aggressiveness or competitive behaviour are still scarce.

Differences in threat postures were found between Swan Geese and hybrids with hybrids performing diagonal neck displays more often and intentional movements less often. This behaviour could be attributed to hybrids alone as diagonal neck and forward threat display are the most common threat postures in Greylag Geese (Johnsgard 1965, Bauer & Glutz von Blotzheim 1968). This might be an indication of intermediate threat displays in hybrids which was not reported before, while intermediate display during courtship has been reported for Red-crested Pochard *Netta rufina* x Ferruginous Duck *Aythya nyroca* (Randler 2003a) and for Shelduck *Tadorna tadorna* x Merganser *Mergus merganser* (Lind & Poulsen 1963).

The proportion of intentional movements was very high in Swan Geese but not in hybrids and could therefore be a behavioural trait that has developed in domesticated animals or has been overlooked in natural populations, because most other studies report low amounts of such threats. Domesticated birds normally live in much denser flocks compared to natural populations, and this behaviour might be beneficial as it reduces costly interactions.

My study provides evidence that hybrids may be competitively equal compared to their parents species and that goose flocks under semi-natural conditions show similar interaction behaviour compared to natural flocks.

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STRESZCZENIE

[Zachowania agresywne gęsi garbonosych oraz ich mieszańców]

W pracy opisano postawy grożenia oraz inne zachowania agresywne w stadzie złożonym z 140 osobników gęsi garbonosej i 13 mieszańców tego gatunku z gęgawą, przebywającym w parku miejskim w Heidelbergu (Niemcy).

Jako zachowanie antagonistyczne opisywano konfrontację między dwoma osobnikami wyrażaną postawami grożenia, przeganianiem lub walką. Wyróżniono 5 rodzajów zachowań agresywnych, większość z nich stanowiły pozy przybierane przez atakujące osobniki. Wynik zachowań opisywano jako: wygrana (gdy drugi osobnik oddalił się), porażka (kiedy osobnik rozpoczynający konfrontacje sam się oddalał), lub bez rozstrzygnięcia (gdy drugi osobnik odwracał się, lub ignorował zaczepki).

Zachowania antagonistyczne stanowiły mniej niż 1% budżetu czasowego poszczególnych osobników. Większość starć wygrywały osobniki inicjujące, zarówno w przypadku gęsi garbonosych jak i mieszańców (Tab. 1). Nie stwierdzono również istotnych różnic między tymi dwiema grupami w wynikach starć, co może sugerować podobną zdolność konkurencyjną. Stwierdzono istotne różnice w częstości rodzajów zachowań agresywnych prezentowanych przez mieszańce i gęsi garbonose (Tab. 2).

Uzyskane wyniki nie wskazują, aby mieszańce były podporządkowane lub dominujące.