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The impact of mass outbreaks of black flies (*Simuliidae*) on the parental behaviour and breeding output of colonial common gulls (*Larus canus*)

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Studies in colonies of common gulls in Poland show that black fly outbreaks can affect breeding success in colonial waterbirds. During massive black fly outbreaks, many pairs of common gulls deserted their nests, both during the incubation period and after hatching. Remaining pairs exhibited less parental care, spent less time at territories and when present, often wheeled above their nests instead of incubating, brooding, or feeding their chicks. Increased absence of adults resulted in increased nest predation by crows and magpies and frequent starvation of broods. Mortality of chicks and adults caused by physical harassment and probably direct loss of blood and body fluids from biting flies was also observed. During black fly outbreak years, loss of clutches and broods increased by 40% to 60%. Low breeding success during outbreak years may limit recruitment of young birds to the colony resulting in long-term population decreases.

1. Introduction

Black flies (Diptera: *Simuliidae*) are small flies (1–6 mm) of worldwide distribution that occur in proximity of streams and rivers. These flies have aquatic larvae and pupae that require running water for their development. As in mosquitoes (*Cullicidae*), males and females feed on plant sap, but females require a blood meal to produce viable eggs (Ross *et al.* 1982, Crosskey 1990). In some years black flies occur in enormous swarms. Studies show that mass outbreaks of blood-feeding insects affect the health and productivity of farm animals (Steelman 1976, Niesiołowski 1980). In tropical and subtropical countries, black flies are of medical importance as they may transmit parasites to animals and people. In the temperate zone, however, their fundamental harm is from nuisance bites resulting from the need of the female to obtain a blood meal. "Blackfly fever",

an illness characterised by an increase in temperature, loss of weight, weakness, decreasing body condition etc. can result (Jamnaback 1973, Niesiołowski 1980). It can also result in death of more sensitive animals. Richard and Davis (1977) reported that *Simulium meridinale* caused the death of numerous turkeys and chickens in Virginia, USA. Black flies are vectors of filaria in ducks (Anderson 1956) and vectors of several species of avian leucocytozoans pathogenic to young ducks and turkeys (Jamnaback 1973). Edgar (1953) found that egg production in hens decreased during attacks of black flies.

Until now, there has been little evidence of the impact of mass outbreaks of blood feeding insects on the behaviour or breeding success of wild birds. Edman *et al.* (1972) noted an increase in defensive behaviour by birds exposed to increased mosquito densities. Smith *et al.* (1998) found that outbreaks of black flies resulted in physical harassment, anaemia and perhaps blood parasite infection (*Leucocytozoon* spp.) and an increase by 27% of nestling mortality in red-tailed hawks (*Buteo jamaicensis*). Hunter *et al.* (1997) reported similar causes of nestling mortality in great horned owls (*Bubo virginianus*). It appears, however, that no one has studied the impact of black fly outbreaks on colonial waterbirds. It seems that in gregarious birds, nesting on a limited area, nesting mortality can be much higher than in solitarily nesting birds of prey. It is also not known whether massive outbreaks of black flies could affect (like food shortages, e.g. Bukacińska *et al.* 1996, Bukaciński *et al.* 1998) breeding behaviour of adults that additionally could increase clutch or brood losses.

In Poland, massive outbreaks of black flies during the spring and summer seasons have been reported every 1–3 years since 1993, especially in large areas along rivers.

In this study, we report the first demonstration of the negative effect of the mass outbreak of black flies on parental behaviour and breeding success in the common gull (*Larus canus*), a colonial species, breeding on the Vistula River in Poland. We attempted to determine if such numerous, regular appearance of these blood feeding insects during consecutive years could be a new, important limiting factor impacting reproductive success in colonial waterbirds in regions of black fly occurrence.

2. Materials and methods

2.1. Study site and study species

This study was carried out in May and June 1995–1998 in two colonies of common gull situated on islands of the Vistula River. The first colony (130–180 pairs) is situated near the village of Kobylnica (51°40´N, 21°35´E) (designated by colony K). The second colony (100–140 pairs) is located 7 km up the river near Tyrzyn (51°39´N, 21°38´E) (designated by colony T). An ongoing investigation of the breeding ecology and behaviour of a colour marked population of common gulls has been conducted since 1988 (Bukaciński 1997, Bukacińska 1998). The studies have established that phenology and age distribution of adults in both colonies are similar. At the Vistula River, corvids (*Corvidae*) were much more a threat to common gull eggs and chicks than were herring gulls (Dyczkowski 1997, Bukaciński 1997, M. Bukacińska & D. Bukaciński, unpubl.).

2.2. The breeding data and a frequency of massive outbreaks of black flies

During egg laying, all nests in both colonies were marked with numbered sticks. Nest were checked every 2 to 4 days to determine the fate of each clutch. Data were recorded for nests where at least one chick hatched, nests where at least one chick survived one week and nests that failed (complete loss). In this study, the following causes of losses were considered: (1) predation (on the basis of egg-shells, observations or disappearance of chicks or eggs), (2) nest desertion (adults absent from the territory, or low egg temperature), (3) low frequency of chick feeding (chick weight decreased or did not change during subsequent days) and (4) other losses (flooded, trampled by cattle, death of an adult, eggs or chicks cooled or overheated, etc.).

Mass outbreaks of black flies were noted in 1996 and in 1998. In both years, they commenced

in the last half of May and continued to mid-June, with a peak in the first 10 days of June. Fly densities were so great that it was impossible to visit the islands without mosquito-netting, and during the fly peaks it was very difficult to work even when such protective measures were used. In 1996, during the peak outbreak, the majority of common gull pairs in both colonies were incubating or had pipping eggs. In 1998, most pairs had newly hatched chicks (0 to 2 days old). Thus, data for incubation and hatching success could be evaluated (1996: $N = 152$ and $N = 79$, from colony K and colony T, respectively) independently from the post-hatching period and first week of chick raising (1998: $N = 33$ and $N = 20$, respectively). Breeding ecology was compared with that during years of low black flies occurrence (i.e. in 1997 incubation period: $N = 128$ and $N = 37$; and in 1995 post-hatching period: $N = 62$ and $N = 24$). As for black fly years, data regarding both periods were treated independently.

2.3. Behavioural observations and statistical analysis

In breeding years with low numbers of black flies, we observed 44 pairs of common gulls during incubation and 28 pairs during the first week after hatching. During years of black fly outbreaks, we observed 20 and 13 pairs, respectively. All pairs were adults that nested in these colonies in previous years. We made observations for 5–7 hours per day for a total of 35–55 hours for each pair. Data recorded included: (1) the time the territory was unattended, (2) how much time parents spent wheeling above their respective territories and (3) chick-feeding frequency per three hours during the first week of life. Since feeding frequency can depend on brood size (Bukacińska 1998), calculations were made per one chick in a brood.

We used the Mann-Whitney *U*-test to compare breeding ecology and behaviour of birds between years with and without black flies. The proportion of full clutch or brood losses between different years or colonies was compared using the χ^2-test. The Wilcoxon signed ranks test was used for comparisons of birds' behaviour before and during black flies outbreaks (Zar 1984).

3. Results

3.1. Behaviour of adults in the years with and without black flies

The mass outbreak of black flies affected the level of parental care both during incubation and after hatching. In the years with high black fly numbers, territories were left unattended for longer periods than in years without black flies (Mann-Whitney *U*-test: $z = 5.9$, $p < 0.0001$ and $z = 5.0$, $p < 0.0001$ for incubation and first week after hatching, respectively; Fig. 1). During peaks of black fly occurrence, adult birds spent more time wheeling above the nest than in the years without black flies (Mann-Whitney *U*-test: $z = 6.3$, $p < 0.0001$ and $z = 5.1$, $p < 0.0001$ for incubation and first week after hatching, respectively; Fig. 1). Parents fed their chicks less frequently (less than half as much) during outbreak years as compared with years without black flies (mean ± SD: 0.59 ± 0.46/3h/chick *vs.* 1.22 ± 0.62/3h/chick; Mann-Whitney *U*-test: $z = 2.9$, $p = 0.003$).

3.2. Behaviour of birds in the incubation period before and during an outbreak

In the period prior to the appearance of black flies (14 days before) behaviour of the adults was similar to that in the years without black flies (Mann-Whitney *U*-test: $z = 0.33$ and $z = 0.26$, NS for the time the territory was left unattended and time birds spent wheeling above the nest, respectively; Fig. 1). The adults left territories unattended for much shorter periods and spent much less time wheeling above the territory than during an outbreak (Wilcoxon test: $z = 3.9$ and $z = 3.9$, $p < 0.0001$, respectively; Fig. 1). These differences did not result from the differences in the incubation stage, since in the years without black flies behaviour of the adults did not differ between the stages of incubation (Wilcoxon test: $z = 1.06$ and $z = 0.65$, NS for the time the territory was left

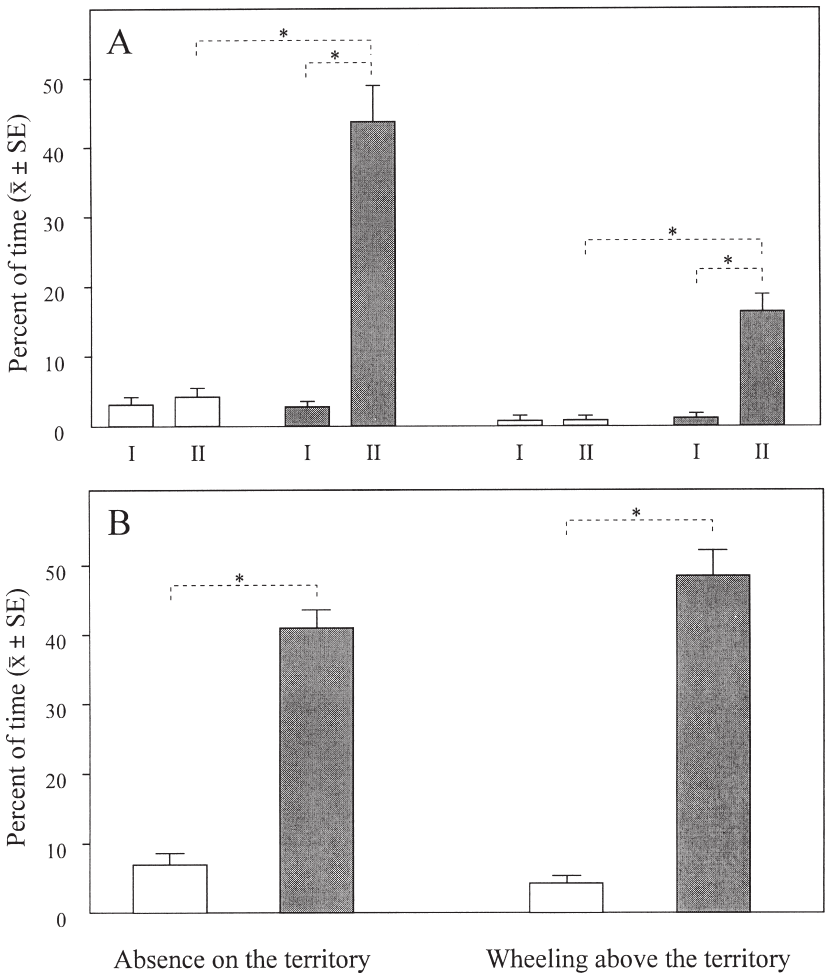

Fig. 1. Behaviour of parents in the years of different black flies occurrence (A) during incubation, (B) during the first week after hatching. Open bars: years without black flies, shaded bars: years of massive outbreaks of black flies. — I: first two weeks of incubation (there is no black flies even in the years of their massive occurrence), — II: third and fourth week of incubation (the period of a peak outbreak in the years with black flies). * $P < 0.0001$, Wilcoxon test for differences within a year and Mann-Whitney *U*-test for differences between years.

unattended and time birds spent wheeling above the nest, respectively; Fig. 1).

3.3. Clutch losses and hatching success

The mean clutch size (from 2.75 ± 0.51 to 2.86 ± 0.40) did not differ between colonies (Mann-Whitney *U*-test: $z = 0.47$ and $z = 0.62$, NS) nor between years (Mann-Whitney *U*-test: $z = 0.20$ and $z = 0.93$, NS). We found, however, that the mean number of eggs in re-layed clutches during an outbreak of black flies (after flooding in mid-May, 1.63 ± 0.72, $n = 30$) was significantly lower than for re-layed clutches in a year without black flies (2.25 ± 0.67, $n = 40$; *t*-test: $t = 3.67$, $p < 0.001$). There were also differences in the proportion of nests with hatching success between years with and without black flies. In the years without black flies, chicks hatched in 67.2% of nests in colony K and in 64.9% of nests in colony T, but in the years of a massive outbreak, chicks hatched only in 21.7% of nests in colony K and in 25.3% of nests in colony T ($\chi^2 = 58.81$, df = 1, $p < 0.0001$ and $\chi^2 = 18.94$, df = 1, $p < 0.001$ for colonies K and T respectively; Table 1). The proportion of successful nests (*see* above) in both colonies was similar in the years without and with black flies respectively ($\chi^2 = 0.01$, df = 1 and $\chi^2 = 0.38$, df = 1, NS; Table 1).

During a year with a black fly outbreak, parents deserted nests more often. This occurred in 30.3% of nests in colony K and in 50.6% of nests in colony T, while in a year without black flies we found only one such case (one adult died in colony K; $\chi^2 = 43.24$, df = 1 and $\chi^2 = 28.59$, df = 1, $p <$

0.0001 for colonies K and T respectively; Table 1). In the years of a massive black fly outbreak, the number of pairs that deserted clutches was higher for colony T (*see* above, $\chi^2 = 9.23$, df = 1, $p < 0.01$), predation (mostly magpies and crows) on entire clutches was found more often in colony K (28.9% *vs.* 7.6% in colony T, $\chi^2 = 13.97$, df = 1, $p < 0.001$; Table 1). During a year without black flies, the level of predation was similar in both colonies ($\chi^2 = 0.01$, df = 1, NS). In colony K, the predation rate was lower (14.1% of nests, $\chi^2 = 8.93$, df = 1, $p < 0.01$), while in colony T it was the same as in a year with an outbreak (13.5%, of nests, $\chi^2 = 1.03$, df = 1, NS; Table 1).

3.4. Brood losses and survival of chicks during the first week after hatching

The effect of a massive black fly outbreak after hatching was similar to that during incubation. In a year without black flies, at least one chick survived the first week in 93.6% of nests in colony K and in 87.5% of nests in colony T (Table 2). During a mass outbreak of black flies, at least one chick survived the first week in only 51.5% of nests in colony K and 25% of in colony T ($\chi^2 = 22.89$, df = 1 and $\chi^2 = 17.63$, df = 1, $p < 0.0001$, respectively; Table 2). Desertion of newly hatched broods we observed only in years with black flies. It was a cause of mortality in 15.2% of nests in colony K and in 40% of nests in colony T ($\chi^2 = 9.92$, df = 1, $p < 0.01$ and $\chi^2 = 11.73$, df = 1, $p < 0.001$, respectively; Table 2). In 18.2% of the nests in colony K and in 35.0% of the nests in colony T, chicks died of starvation (because of very low feeding frequency). This effect was not observed in the years without black flies ($\chi^2 = 12.03$, df = 1, $p < 0.001$ and $\chi^2 = 9.99$, df = 1, $p < 0.01$, for colonies K and T respectively). In colony K, we also found greater predation by magpies on the entire broods during the outbreak (12.1% vs. 1.6%

Table 1. The fate of clutches of common gulls up to hatching in the years with and without massive outbreaks of black flies. *N* = number of nests. For other explanations *see* Material and methods.

Clutch fate	Years with black flies		Years without black flies	
	Colony K N (%)	Colony T N (%)	Colony K N (%)	Colony T N (%)
Laid	152	79	128	37
Hatching success	33 (21.7)	20 (25.3)	86 (67.2)	24 (64.9)
Deserted	46 (30.3)	40 (50.6)	1 (0.7)	0 (0)
Predated[1)]	44 (28.9)	6 (7.6)	18 (14.1)	5 (13.5)
Other losses[1)]	29 (19.1)	13 (16.5)	23 (18.0)	8 (21.6)

[1)] Only full clutch losses.

Table 2. The fate of broods of common gulls during the first week of chick's life after hatching in the years with and without massive outbreaks of black flies. *N* = number of nests. For other explanations *see* Material and methods.

Brood fate	Years with black flies		Years without black flies	
	Colony K N (%)	Colony T N (%)	Colony K N (%)	Colony T N (%)
Hatching success	33	20	62	24
With chicks after 1 week	17 (51.5)	5 (25.0)	58 (93.6)	21 (87.5)
Deserted	5 (15.2)	8 (40.0)	0 (0)	0 (0)
Starved[1)]	6 (18.6)	7 (35.0)	0 (0)	0 (0)
Predated[1)]	4 (12.1)	0 (0)	1 (1.6)	1 (4.2)
Other losses[1)]	1 (3.0)	0 (0)	3 (4.8)	2 (8.3)

[1)] Only full brood losses.

of nests in years without black flies; $\chi^2 = 4.77$, df = 1, $p < 0.05$). In colony T, the black flies outbreak did not affect predation rate ($\chi^2 = 0.85$, df = 1, NS). The level of brood losses caused by predation in this colony was lower than in colony K (one case during two years; $\chi^2 = 4.31$, df = 1, $p < 0.05$; Table 2).

4. Discussion

Huge densities of black flies are very typical for subarctic areas (taiga) (Niesiołowski 1980). Birds' species that nest there most often complete their breeding cycle before the outbreak of these insects (M. Gromadzki, pers. comm). Thus, the effect of black flies on the breeding ecology of birds in the taiga region is probably not very important. In regions of moderate climate in Europe, the hyperabundant densities of black flies is a recent development (*see* Niesiołowski 1980). The first massive black fly outbreak at the Vistula River occurred in 1993, and subsequent outbreaks occurred in the last half of the 1990s. This may be related to more frequent precipitation and higher temperatures recorded lately during the spring and summer seasons (M. Bukacińska & D. Bukaciński, unpubl.). These are, as suggested by Smith *et al.* (1998), the environmental conditions that favour the occurrence of black flies. Also, the distribution of adult black flies may be influenced by distribution of the blood source (McCreadie & Adler 1998). This factor, coupled with the black fly need for running water make colonial waterbirds susceptible to attacks. This is supported by our study in the colonies of common gulls, where the clutch and brood losses induced by these insects were several times higher than in solitary nesting species (Forrester *et al.* 1994, Hunter *et al.* 1997, Smith *et al.* 1998).

Most studies suggested that blood-feeding insects such as blowflies (*Protocalliphora*) contribute to an overall weakened condition of nestlings (e.g. Tirrell 1978, Bortolotti 1985, Hurtrez-Bousses *et al.* 1997a, 1997b), but massive infestation by black flies primarily increased (indirectly or directly) mortality of eggs or chicks (Smith *et al.* 1998, this study). Physical harassment often led to nest desertion by adults, both during incubation and after hatching (15%–50% of pairs in the colony). A similar pattern was observed in colonies of other gull species on the Vistula River. Among 22 herring gull pairs (*L. argentatus*) nesting in colony T in 1998, all incubating pairs (13) deserted nests soon after the black fly outbreak (D. Bukaciński & M. Bukacińska, unpubl.). In a colony of black-headed gulls (*L. ridibundus*) 50 km south of our study area, the attack of black flies caused desertion of a colony by all 350–400 pairs (incubating or caring of hatchlings) (W. Nowicki, pers. comm.).

Biting of flies, at least in several cases, directly caused the death of adults. In 1998, during the first ten days of the massive outbreak of black flies, nine adult common gulls died, whereas in years without insects, at most 2–3 adults were found dead per breeding season (D. Bukaciński & M. Bukacińska, unpubl.). For some deserted and poorly fed chicks, dehydration and anaemia, not starvation, appeared to be direct causes of mortality (Bortolotti 1985, Sabrosky *et al.* 1989, Smith *et al.* 1998). All dead birds (both adults and chicks) had extensive dermatitis, mainly on the head, around the eyes and near the ears, and on the neck. Smith *et al.* (1998) suggested that downy chicks are particularly susceptible to black fly bites. Our data seem to support this suggestion. Among chicks that hatched during the outbreak, only one common gull brood and none of seven broods of herring gulls survived. According to Davidar and Morton (1993), feather development and maturation of the immune system protects older chicks to some extent against attacks of biting insects.

Indirect breeding failures caused by black flies resulted from the increased predation rate and chick starvation. Insects' attacks caused parents to leave territories unattended for longer periods of time. Moreover, even if adults were at the territory, the incubation or brood care was not effective. Birds were observed frequently taking flight and wheeling above the territory. Such nest care was insufficient to prevent magpie and crow predation. On several occasions we observed successful attacks on eggs and small chicks when parents were wheeling in the air. During the outbreak, adults also fed chicks much less frequently. This caused brood starvation.

The cumulative effect of black fly attacks in colonies of common gulls reduced hatching success at least by 40%–45% and chicks survival dur-

ing the first week after hatching by 45%–60%. Clutch size of re-layed clutches was also smaller than usual.

Until recently, population numbers of gulls nesting on the Vistula River were regulated by nest site availability, pasturage, floods and predation (Bukaciński & Bukacińska 1994, 1995). The mass appearance of black flies in the Vistula River system appears to be a new factor. By causing reduction of recruitment of young birds into the colony, these insects may have a significant impact on the regulation of population numbers in these birds. Their impact on breeding success of other waterbirds should be investigated.

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