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Time budget of common cranes (Grus grus) varies between habitats: implications for management

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Abstract

Common cranes (*Grus grus*) of the growing population in Finland form flocks on cultivated fields to forage in the autumn after the breeding season, in preparation for a successful migration. However, human-crane conflicts can arise when cranes cause crop damage, and for management purposes, it is important to prevent such conflicts. To minimize crop losses, one strategy is the creation of artificial feeding fields in high-use areas. Our study area, Söderfjärden, Ostrobothnia, on the west coast of Finland, is the most important staging area for cranes in the country. We compared the time allocation in the most attractive habitats in this area, investigated the changes in flock size during the day, and considered the management implications. Cranes used the two top-rated habitats (barley fields and grasslands) for clearly different purposes: barley fields for feeding and grasslands for resting. Flock size increased from the early morning until the evening when cranes dispersed from the area to roost. This could be a result of a trade-off between food intake and risk-sensitive behaviour and predator avoidance, although at present the predation risk in the area is low. This study highlights the importance to make artificial feeding habitats to fulfil various needs of cranes while minimizing crop loss and potential conflicts with humans.

Keywords: common crane, Gruidae, conservation, foraging, habitat selection, vigilance

Introduction

Cranes (Gruidae) are generally a threatened group of birds with 11 of 15 species considered critically endangered, endangered, vulnerable, or near threatened (Austin et al. 2018, IUCN 2022). The remaining species are considered of least concern due to abundant population sizes including the common crane (*Grus grus*), whose overall population is increasing as is its population in Europe (IUCN 2022). In recent decades, many large-bodied herbivorous avian species in Europe are recovering from a decline in population size (Fox and Madsen 2017, Fox et al. 2017, Elmberg et al. 2020). However, conservation practices that have been so successful at increasing common crane populations, have unfortunately led to crane-human conflicts because of the local abundance of the birds in agricultural areas.

Human-crane conflicts can arise when cranes cause crop damage (Sudgen et al. 1988, McIvor and Conover

1994, Borad et al. 2001, Montràs-Janer et al. 2019). The monetary compensation from the governments to the farmers for this damage is continuously growing worldwide, including Finland (Alonso et al. 2018, Ympäristöministeriö 2019). Crane diet composition depends on the season and availability of food. During their breeding, common cranes mostly forage omnivorously, e.g. on frogs, fish and berries (Nowald et al. 2018). During the spring and autumn migration, however, common cranes forage mainly on grains and potatoes in cultivated fields. Some crane species are quite dependent on agriculture. For example, most of the world's near-threatened black-necked cranes (G. nigricollis) feed during winter almost entirely on waste barley or winter wheat (Austin et al. 2018). Cranes can also cause damage to newly sown fields in the spring and unharvested fields in the autumn (Lundin 2005, Niemi et al. 2009). In the wintering areas, cranes are also mostly herbivorous (Cramp and Simmons 1980, Aviles et al. 2002). Usually,

when common cranes arrive at the wintering areas in autumn, most of the crops have been harvested, but if not, cranes can decrease yields of crops, such as corn and wheat (Végvári 2002, Nowald et al. 2018).

In Finland, after the conclusion of the breeding season in the summer, common cranes congregate on cultivated fields in the autumn to forage and replenish fat reserves before their long migration to Southern Europe, North Africa, and Middle East (Leito et al 2015). As in many other countries, the Finnish Ministry of the Environment subsidizes farmers for crop losses caused by the cranes (Lundin 2005). However, due to the increasing population of cranes, it is now becoming crucial to assess the damage and implement mitigation measures. Yet, there is a general gap in knowledge of the foraging ecology of cranes in the staging areas in Northern Europe, although a few studies have been already carried out on this topic (Leito et al. 2008). The lack of knowledge of the habitat and food requirements of the common cranes makes it difficult to develop management plans. Artificial feeding fields have been suggested as a means to prevent crop losses (Végvári 2002), but such solutions require knowledge of habitat use and feeding behaviour. Artificial feeding fields are used to attract the cranes away from the valuable crops.

The availability of both food and habitats for cranes varies along the migratory flyways. For example, in autumn gathering areas in Sweden and Finland, barley (*Hordeum vulgare*) is available and preferred by common cranes (Lundin 1995, Niemi et al. 2009). By the time cranes migrate southwards, barley fields have already been ploughed and thus this preferred food is not available. In staging areas in Estonia, the main food of common cranes usually consists of summer wheat, winter wheat and winter rye (Leito et al. 2008), while in the staging area in Hungary, they feed on waste grain in maize stubble (Végvári 2002) and in the wintering areas in Spain cranes mainly feed on stubble fields or the acorns of holm oaks (*Quercus robur*; Alonso et al. 1994, Diaz et al. 1996, Aviles et al. 2002).

For management purposes, food requirements and foraging habitats of cranes are not the only important factors. It is also necessary to know how the birds use surrounding habitats for other essential functions, such as resting, maintenance, vigilance, etc., and how these behaviours influence how cranes are selecting between potential foraging habitats. These related habitats are very important for crane behaviour expression, as in many other bird species (Mysterud and Ims 1998, Nowald et al. 2018). If another important habitat is identified close to crop fields that are attractive for cranes, it might be developed into an attractive artificial feeding field (Niemi et al. 2009).

Flock size, behaviour and daily variation in the activity of cranes also affect habitat use. In earlier studies, Alonso and Alonso (1992) observed that wintering cranes shifted from risk-prone foraging with a higher food intake rate in the morning to risk-averse foraging with a lower intake rate in the evening. Cranes formed smaller flocks in the morning and aggregated into larger flocks during the afternoon. Knowledge of this type of behaviour could be of importance in preventing crop loss, since the increasing common crane population in Finland can result in large concentrations of the species, which leads to crop damage (Nowald et al 2018).

In the present study we aimed to 1) compare the time allocation of common cranes in the most attractive habitats of an autumn staging area in Finland, 2) investigate whether the previously reported pattern of an increase in flock size during the day also holds in this area, and 3) discuss the management implications.

Materials and methods

Study area

Based on staging birds, Söderfjärden, Ostrobothnia (63°00'N, 21°35'E), on the west coast of Finland, is the most important autumn staging area for a large number of cranes in the country (Autio et al. 2020). The landscape mainly consists of agricultural fields covering 2,300 ha, in a round-shaped ancient meteorite crater. The attractiveness of the area for birds might be due to its high production of barley (4,500–5,000 kg/ha) compared to the average level in Finland of 3,200 kg/ha (Lundin 2005). Our study site covered half of the Söderfjärden area in which it is possible to observe crane behaviour and habitat use. The other side of the area is inaccessible because of the lack of roads. There was little human disturbance affecting our surveys. If there were some humans in the fields, they were over one kilometre from the observed birds.

The first staging cranes arrive at Söderfjärden in August, and the last cranes leave the area in the middle of October. The main migration peak usually takes place at the end of September. The main crop harvesting period extends from mid-August to early September, when there are usually 1,000–3,000 cranes in the area (Lundin 2005). Therefore, the amount of crop damage may have depended on how much of the cereal has been threshed before the cranes arrive.

Data collection

The study was carried out from the $18^{th}-29^{th}$ August 2008. The fields of the study area were mainly unharvested at this time, while there were over a thousand cranes in the area and the risk of crop damage was large. The cranes flew out to roosting areas in the Merenkurkku archipelago 5 to 10 kilometres away every evening and returned to Söderfjärden in the early morning. We observed them every day from 07:00 a.m., when they arrived in the study area, until 07:00 p.m., when most of the birds were leaving the area. Observations of crane behaviours were carried out from a stationary car with a 25–75× spotting scope from a distance of 200 to 400 m.

Cranes usually congregated along the border of their chosen field, forming elongated flocks. We noticed no changes in crane behaviour upon our arrival, but in order to avoid any disturbance we always waited for five minutes before recording their behaviour.

In the earlier, preliminary report, it was found that in the study area barley and grass were important habitats for cranes (Niemi et al. 2009), and we focused our time allocation survey on these two habitat types (barley ca. 700 ha, grass ca. 30 ha). The other crops cultivated in the area included wheat, oats, potatoes, rye, rapeseed, sugar beet and peas, with some fields being left fallow (Niemi et al. 2009).

Following the recommendations of Alonso and Alonso (1992, 1993), we recorded the date, time, weather, flock size, number of juveniles and type of ground cover (grass or unharvested barley). For each flock, we recorded with spotting scopes the behaviour of 1 to 10 adults and 1 to 5 juveniles when possible. The numbers recorded were approximately proportional to flock size. Individuals were chosen at regular distances along the flock's longest diameter to avoid biases due to the position of individuals in the flock. Feather characteristics allowed us to discriminate between adults and juveniles (first-year birds) (Cramp and Simmons 1980). The social status of individuals was also noted (adult with juvenile or without). However, during the field study, there were so few families in the area that we could not study juveniles and parents separately, and we excluded families including juveniles and parents from the analyses due to the limited observations of common crane families in our dataset.

During the field study, we observed the behaviour of 485 individuals. We excluded the observations of juveniles and the adults with juveniles. In total, the time budget of 385 individuals was included in the statistical analysis. Six behavioural categories were defined: feed-



Figure 1. Daily average allocation of time to various activities $(\pm SE)$ among cranes on barley and grass habitats

ing (head down), vigilance (head-up), preening, moving, resting (head bent to the side or a head-up posture lasting more than one minute) and aggression. Each individual was continuously followed for 100 seconds. We did not record the time spent flying, because it could not be clearly classified as an activity associated with a particular habitat type.

During the study the flock size of cranes varied from 3 to 550 individuals. During the field studies, we made observations of 82 crane flocks which might have partly consisted of the same individuals in different composition (Figure 1). During the field studies, the number of cranes at Söderfjärden was counted in the evening from the middle of the fields when cranes started their roost flight.

Statistical analyses

We formulated generalised linear mixed models (GLMMs) in the statistical software R (R Core Team 2020) with "glmmTMB" package (Brooks et al. 2017). As the time the cranes spent on each type of behaviour are non-negative continuous values, i.e. [0, ... 100], we applied: 1) GLMMs with a binomial distribution to analyse the probability of common cranes exhibiting a behaviour, and 2) GLMMs with a Gamma distribution to analyse the data when cranes having such type of behaviour. Although in this study we aimed at investigating the time budget of cranes between habitats, we noticed other factors also had effects on the time budget of cranes in data exploration. The fixed effects we included in our models were: 1) the vegetation types (barley field or grassland), 2) the location of the bird in the field (in the middle of the flock, or at the edge of the flock), 3) the distance to the nearest bird, 4) the flock size classes (< 10 birds, 10-25 birds, 26-50 birds, > 50 birds), 5) the time of the day of each observation, and 6) the weather (rainy, or not rainy). As the birds within a flock may have similarity in their behaviours, we included the flock ID as random effects. We conducted backward selection with the function "step" to select the optimal model. In general, the cranes spent little time for sleeping and aggression: 45 birds out of 414 observations spent time in sleeping, and 16 birds had aggression behaviour. Thus, the data is too scarce to allow statistical tests.

Results

Foraging behaviour

Cranes preferred foraging in barley fields to grassland foraging; they were less likely to forage in grasslands (Estimated $\pm SD = -3.27 \pm 0.43$, *p*-value < 0.001, Table 1, Figures 1, 2) and spent less time foraging in grasslands (Estimated $\pm SD = -0.64 \pm 0.15$, *p*-value < 0.001, Table 2). Although there was no significant difference between the locations of the flock, the location of the flock could not be dropped from the optimal binary model. Cranes were more likely to forage with increasing distance to another bird but without statistical significance (Esti-

	Foraging	Vigilance	Preen	Moving
Grassland	Estimated $\pm SD = -3.27 \pm 0.43$	-	Estimated ± SD = 2.53 ± 0.33	Estimated \pm SD = -1.09 \pm 0.25
	Z-value = -7.55		Z-value = 7.60	Z-value = -4.30
	<i>p</i> -value < 0.001		<i>p</i> -value < 0.001	<i>p</i> -value < 0.001
At the edge of	Estimated \pm SD = 0.44 \pm 0.28 E	stimated \pm SD = 0.81 \pm 0	.52 Estimated ± SD = -0.40 ± 0.26	-
the group	<i>Z</i> -value = 1.57	Z-value = 1.55	Z-value = -1.54	
	<i>p</i> -value = 0.117	<i>p</i> -value = 0.121	<i>p</i> -value = 0.121	
Flock size	-	-	-	-
Distance to the	Estimated \pm SD = 0.27 \pm 0.14	-	Estimated \pm SD = -0.32 \pm 0.14	Estimated \pm SD = 0.23 \pm 0.11
nearest bird	Z-value = 1.86		Z-value = -2.18	Z-value = 2.09
	<i>p</i> -value = 0.061		<i>p</i> -value = 0.028	<i>p</i> -value = 0.036
Time of the	Estimated \pm SD = -0.27 \pm 0.16	-	-	Estimated \pm SD = -0.34 \pm 0.12
day	Z-value = -1.80			Z-value = -2.74
•	<i>p</i> -value = 0.072			<i>p</i> -value = 0.006
Rainy weather	-	-	Estimated \pm SD = -1.28 \pm 0.41	-
			Z-value = -3.08	
			<i>p</i> -value = 0.002	
Random effect: Flock ID	0.732	0.52 ²	0.572	0.37 ²

Table 1. The results of optimal binary models for each tested behaviour

Note: The models analyze the probability of cranes having each behaviour. "In the middle of the group", "non-rainy weather", and "barley field" were set as the reference levels of "location of the bird", "weather", and "vegetation type", respectively. "-" means the factor is not excluded in the optimal model.

Table 2. Results of optimal gamma models for each tested behaviour

	Foraging	Vigilance	Preen	Moving
Grassland	Estimated ± SD = -0.64 ± 0.15 Z-value = -4.30 p-value < 0.001	-	Estimated ± <i>SD</i> = 0.33 ± 0.10 <i>Z</i> -value = 3.31 <i>p</i> -value < 0.001	Estimated ± <i>SD</i> = 0.76 ± 0.18 <i>Z</i> -value = 4.16 <i>p</i> -value < 0.001
At the edge of the group	· -	-	-	-
Flock size	-	See texts	-	-
Distance to the nearest bird	-	Estimated \pm SD = -0.07 \pm 0.04 Z-value = -1.48 p-value = 0.138	-	-
Time of the day	-	Estimated $\pm SD = 0.09 \pm 0.05$ Z-value = 1.76 p-value = 0.077	-	-
Rainy weather	Estimated \pm SD = 0.27 \pm 0.14 Z-value = 1.86 p-value = 0.062	-	-	-
Random effect: Flock ID	0.002	0.17 ²	0.00 ²	0.37 ²

Note: The models analyse how the environmental factors affected the time cranes spent on each behaviour, under the condition that they have such a behaviour. "In the middle of the group", "non-rainy weather", and "barley field" were set as the reference levels of "location of the bird", "weather", and "vegetation type", respectively. "–" means the factor is not excluded in the optimal model.

mated $\pm SD = 0.27 \pm 0.14$, *p*-value = 0.062, Table 1), but the distance to another bird was not included in the optimal model regarding how much time cranes spent foraging. Our optimal binary model shows cranes had a higher probability of foraging in the morning than in the afternoon (estimated parameter $\pm SD = -0.29 \pm 0.16$, *p*-value = 0.072, Table 1), but the time of day was not included in the optimal Gamma model (Table 2). The flock size was not included either in the optimal binary model or in the optimal Gamma model (Tables 1 and 2).





We could not do reliable statistical analysis, because the data is unbalanced: 24 observations in harvested barley fields, 200 observations in non-harvested barley fields, 142 observations in harvested grasslands, and 48 observations in non-harvested grasslands.

Vigilance

The location of the crane flock was the only factor included in the optimal binary model of vigilance; cranes were more likely to have vigilance behaviour at the edge of fields than in the middle of a field, but without statistical significance (Estimated $\pm SD = 0.81 \pm 0.52$, p-value = 0.121, Table 1). In the optimal Gamma model, only the flock size, distance to another bird, and time of the day were included. There was no significant difference among flock sizes < 10 birds, 10-25 birds, and 26-50 birds. Cranes spent significantly less time on vigilance in a flock with over 50 birds than in a flock with < 10 birds (Estimated $\pm SD = 0.39 \pm 0.19$, *p*-value = 0.037) and in a flock with 26–50 birds p-value = 0.017), (Estimated $\pm SD = 0.35 \pm 0.15$, but no difference compared to a flock with 10-25 birds $(0.18 \pm 0.14, p$ -value = 0.193). Although the distance to the nearest bird could not be dropped from the model, its effect on how much time cranes spent on vigilance was close to zero and insignificant (Estimated $\pm SD = -0.07 \pm 0.04$, p-value = 0.138, Table 2). The cranes spent more time being vigilant in the afternoon than in the morning, although without statistical significance (Estimated $\pm SD = 0.09 \pm 0.05$, *p*-value = 0.077, Table 2).

Preening

Ourresultsshowthat, compared with barley fields, cranes were more likely to preen (Estimated $\pm SD = 2.53 \pm 0.33$, *p*-value < 0.001, Table 1, Figure 1) and spent more time preening in grassland (Estimated $\pm SD = 0.33 \pm 0.10$, *p*-value < 0.001, Table 2). Cranes were less likely to preen at the edge of the field (Estimated $\pm SD = -0.40 \pm 0.26$, *p*-value = 0.121, Table 1) than in the middle of the field, but without statistical significance. Cranes were more likely to preen with the decreasing distance to the nearest bird (Estimated $\pm SD = -0.32 \pm 0.14$, *p*-value = 0.028) and when it was rainy (Estimated $\pm SD = -1.28 \pm 0.41$, *p*-value = 0.002, Table 1). Flock size and time of the day were not included either in the optimal binary model or the optimal Gamma model.

Moving

Compared with barley fields, cranes had significantly lower probability to move in grasslands (Estimated $\pm SD = -1.09 \pm 0.25$, *p*-value < 0.001, Table 1); however, when cranes moved in the observed fields, cranes spent more time moving in grasslands (Estimated $\pm SD = 0.76 \pm 0.18$, *p*-value < 0.001, Table 2) than in barley fields. The probability of crane moving increased with increasing distance to the nearest bird (Estimated $\pm SD = 0.23 \pm 0.11$, *p*-value = 0.036, Table 1). Cranes had a higher probability to move in the morning than in the afternoon (Estimated $\pm SD = -0.34 \pm 0.12$, *p*-value = 0.006, Table 1). The location of the flock, flock size, and weather were not included in the final models (Tables 1 and 2).

Flock size

There were no significant differences in flock size < 10 birds nor in > 50 birds between grasslands and barley fields (Table 3). However, flock sizes 10–25 birds tended to use grasslands more than barley fields (Estimated $\pm SD = 13.23 \pm 5.89$, *p*-value = 0.024), while 26–50 birds used grasslands less than barley fields (Estimated $\pm SD = -13.86 \pm 5.51$, *p*-value = 0.011, Table 3, Figure 3). There was no statistical difference in the flock



Figure 3. Group size of cranes (± SE 99.9%) in barley and grass

Table 3. The relationship between flock sizes and habitats and time of the day

	Flock sizes			
	< 10 birds	10.25 birds	26 50 birds	> 50 birdo
		10-25 bitus	20-50 birds	> 50 bilus
Grassland	Estimated \pm SD = 0.71 \pm 3.46	Estimated ± SD = 13.23 ± 5.89	Estimated $\pm SD = -13.86 \pm 5.51$	Estimated \pm SD = 1.81 \pm 6.23
	Z-value = 0.20	Z-value = 2.24	Z-value = -2.51	Z-value = 0.29
	<i>p</i> -value = 0.837	<i>p</i> -value = 0.024	<i>p</i> -value = 0.011	<i>p</i> -value = 0.770
Time	Estimated $\pm SD = -0.56 \pm 1.92$	Estimated $\pm SD = -0.15 \pm 1.69$	Estimated \pm SD = -1.50 \pm 2.71	Estimated \pm SD = 11.07 \pm 4.30
	Z-value = -0.293	Z-value = -0.09	Z-value = -0.55	Z-value = 2.57
	<i>p</i> -value = 0.769	<i>p</i> -value = 0.927	<i>p</i> -value = 0.579	<i>p</i> -value = 0.009
Random effect:	61.44 ²	81.39 ²	81.46 ²	28.99 ²

Note: "Barley field" was set as the reference level.

sizes < 10 birds, 10–25 birds, and 26–50 birds during the day (Table 3), but flocks > 50 birds tended to form in the evening (Estimated $\pm SD = 11.07 \pm 4.30$, *p*-value = 0.009, Figure 4).



Figure 4. The mean group size $(\pm SE)$ varied during the day in barley and grass habitats

Discussion

Barley and grass habitats in different use

Our new finding was the clear separation in the use of the two top-rated habitats of cranes: barley fields for feeding and grasslands for resting. Barley has also been found to be favoured by common cranes in other stopover areas (Lundin 2005), because the energy content of barley is high, allowing cranes to store energy before migration. Cranes visited several fields each day similar to what Alonso et al. (1995) found in wintering areas in Spain. Interestingly, also harvested barley fields seemed to be used for feeding as much as the non-harvested ones. This resembles the situation in central Europe where cranes have been foraging on agricultural lands for at least 200 years, but conflicts with farmers rarely occurred because the cranes fed on the stubble fields after harvest in autumn (Nowald et al. 2018). The duration of our observations of each individual was quite short, but probably do not affect our main findings.

In a staging area in Hungary, crane flocks have been observed to use natural grasslands to hunt for invertebrates at the grassroots (Végvári 2002). In our study, the grass habitat was mostly used for resting, and only a few cranes in the flocks were observed to feed, possibly on earthworms or other invertebrates. As the grass habitat still seemed to be intentionally selected, grasslands must have offered some other advantages for cranes. In our study, common cranes spent less time on vigilance in a flock with over 50 birds than in the other two smaller flocks. In many studies on birds and mammals, the minimization of predation risk has been found to be more important than the maximization of energetic gain (Moody et al. 1996, Cimprich et al. 2005), and safety from predators or other disturbances also seems to be one important element of crane habitat selection (Franco et al. 2000). Safety during the daytime sleeping period is especially important for many resting birds (Németh and Moore 2007). However, an individual's state influences its behaviour (McNamara and Houston 1986).

Grasslands and unharvested barley fields are structurally different types of habitats. Grasslands are open habitats with short vegetation, and it is more difficult for predators to hide there. Unharvested barley fields probably offer more cover for an approaching predator. Thus, grasslands might be more suitable habitats for preening and resting. For example, in a habitat selection study in Portugal, cranes avoided shrubby vegetation (Franco et al. 2000). When cranes are preening in grasslands, they are still above the growth, and low-quality detection (head-down) (*sensu* Lima and Bednekoff 1999, Beauchamp 2003) is possible.

At present, predation risk in the study area is low: only in exceptional cases foxes (*Vulpes vulpes*) or golden eagles (*Aquila chrysaetos*) can pose a real threat to cranes, and the population of wolves is low (Heikkinen et al. 2022). However, cranes might be adapted to past predation pressure of the previous centuries (Littlefield 1995) or that of other areas. The present low predation pressure is a relatively recent phenomenon resulting from the high anthropogenic influence in the area. In nearby breeding areas, cranes may come into contact with increasing populations of large predators such as wolves (*Canis lupus*). Predator abundance also varies along the migration route, and crane behaviour may not only be adapted to the conditions of one part of the flyway (Cimprich 2005).

This habitat use of cranes appears to have features of landscape supplementation (Dunning et al. 1992). The barley patches are located in a portion of the landscape that contains grassland patches as additional resources. As cranes do not necessarily need a grass habitat for feeding or resting, it might be considered as a substitutable resource.

Flock size

The optimal flock size varies in different situations (Pulliam 1973, Elgar and Catterall 1981). During our study period, flock size varied during the day, tending to increase towards the evening in both grassland and barley fields. This pattern has also been observed in earlier studies conducted in wintering areas (Alonso and Alonso 1992, Alonso et al. 1995). Vigilance has been predicted to decrease with flock size due to increased predation detection and dilution of predation risk in larger flocks (Beauchamp 2008). However, the relationship between vigilance and flock size is a complicated one (Lima and Dill 1990, Frid 1997), and,

in nearly one-third of all published studies, the relationship has not been found (Beauchamp 2003). With our data, we cannot demonstrate firmly why the flock size effect is not found in grasslands. But because cranes flock in the grassland to rest, it is reasonable to assume that the predation risk is lower there. In an earlier study of cranes, Aviles and Bednekoff (2007) found a flock size effect in both habitats (cereal crops and set aside areas) they studied. However, in our study, grassland habitats were clearly more open than barley fields. In this case, the need for being vigilant decreases because the cranes are safe enough (Frid 1997), and this masks the relationship between vigilance and flock size. Cranes do not need the benefits of larger flocks (Aviles and Bednekoff 2007). In barley visibility is low, and flock size may have greater importance in crane behaviour.

Generally, competition can be a reason for individuals to form smaller flocks (Caraco et al. 1980), and it could be one of the reasons why cranes formed small flocks in the mornings. However, hardly any aggression (0.23% of the time budget) was observed, which indicates that competition and scrounging may not be important in the area. In the densely populated wintering areas in Spain, cranes also spent only a mean of 0.33% of the daytime in aggressive behaviour (Alonso and Alonso 1993).

Earlier studies have discussed the flock size effects on crane behaviour and assumed that cranes take greater risks during the mornings to become satiated (Alonso and Alonso 1992). This agrees with the predictions of risk-sensitive foraging models (Stephens 1981, Stephens and Krebs 1986). The reason why cranes congregate in larger flocks in the afternoon is more obvious than the forming of small flocks in the mornings. In a large flock, the predation risk is lower, cranes are able to become satiated and food availability is also sufficient for larger flocks. Cranes also prepare for the roost flight or the beginning of the migration in large flocks.

Applications for management

When planning to manage crane areas by providing feeding fields, we should take both habitat needs and social behaviour into consideration when making suitable habitats. In this way, as large a proportion of cranes as possible may gather in the same area. However, it is possible that cranes do not select their foraging and resting areas solely on the basis of the cereal type (e.g. barley or wheat) or habitat type (e.g. grass or barley), but that they thrive in places where abundant food of high quality, such as barley, are combined with safety features. The concept of having alternating grassland and cereal field sections is incorporated into the present model of bird fields in Finland (Ympäristöministeriö 2019).

In our study area, both in barley fields and grasslands, cranes were usually located along a ditch that offers drinking water, so they did not have to move further away to drink between feeding bouts. Apparently, the availability of water influenced the habitat choice of cranes. Water has also been found important in wintering areas (Franco et al. 2000).

The aptitude of cranes to spread out over the fields in the morning could be a problem with feeding fields, because it is difficult to attract cranes to a single area. This would be easier to achieve in an area where artificial feeding fields are clearly isolated from other fields. In such areas, cranes could be easily scared away from crop fields and onto the feeding fields. However, in non-isolated areas such as our study site, artificial feeding fields could offer benefits if food for cranes (e.g. barley) is provided in a safe area where water is also available. This method has been generally used in Finnish policy to manage agriculture fields for cranes (Autio et al. 2020).

Considering management, the results of feeding behaviour in harvested and not harvested barley fields are interesting. Cranes seemed to be actively feeding in both habitats. Thus, it would be favourable if farmers and other relevant stakeholders identify the areas favoured by cranes with their local knowledge and harvest some of the fields earlier. In these harvested fields, cranes then could forage without disturbance since they are not causing crop damage. Also, some grain can be left in the field during harvest, so that cranes spend less time in unharvested fields (Austin and Sundar 2018). This study highlights the necessity of making artificial feeding habitats for cranes in late summer to avoid human-crane conflicts when helping cranes prepare for a successful migration in wildlife conservation.

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Authors contributions

SB and PN designed the study. SB collected the data, plotted the figures, and wrote the first draft of the manuscript. WL conducted data analysis, commented and revised the manuscript. PN supervised SB conducting the study, revised and added new references to the manuscript.

References

- Alonso, J.C. and Alonso, J.A. 1992. Daily activity and intake rate patterns of wintering common cranes *Grus grus*. Ardea 80: 343–350.
- Alonso, J.C. and Alonso, J.C. 1993. Age-related differences in time budgets and parental care in wintering common cranes. *The Auk* 110: 78–88.
- Alonso, J.C., Alonso, J.A. and Bautista, M.B. 1994. Carrying capacity of staging areas and facultative migration extension in common cranes. *Journal of Applied Ecology* 31: 212–222.

- Alonso, J.C., Alonso, J.A., Bautista, L.M., and Muñoz-Pulido, R. 1995. Patch use in cranes: a field test of optimal foraging predictions. *Animal Behaviour* 49: 1367–1379.
- Alonso, J.C., Alonso, J.A. and Bautista, L.M. 2018. A Review of the Crane-Agriculture Conflict at Gallocanta Lake, Spain. In: Austin, J.E., Morrison, K.L. and Harris, J.T. (Eds.) Cranes and Agriculture: A Global Guide for Sharing the Landscape. Baraboo, Wisconsin, USA: International Crane Foundation, p. 272–279.
- Austin, J.E. and Gopi Sundar, K.S. 2018. Methods to Reduce Conflicts between Cranes and Farmers. In: Austin, J.E., Morrison, K.L. and Harris, J.T. (Eds.) Cranes and Agriculture: A Global Guide for Sharing the Landscape. Baraboo, Wisconsin, USA: International Crane Foundation, p. 117–141.
- Austin, J.E., Morrison, K.L. and Harris, J.T. (Eds.) 2018. Cranes and Agriculture: A Global Guide for Sharing the Landscape. Baraboo, Wisconsin, USA: International Crane Foundation, 303 pp.
- Autio, O., Heliölä, J. and Rinkineva-Kantola, R. 2020. Lintupellot rauhoitettujen lintulajien aiheuttamien satovahinkojen ennaltaehkäisevänä keinona [Bird fields as a preventive measure against crop damage caused by protected bird species]. Rapporter 16/2020. Seinäjoki: NTM-centralen i Södra Österbotten, 46 pp. (in Finnish with English abstract). URL: http://urn.fi/URN:ISBN:978-952-314-858-1.
- Aviles, J.M., Sanchez, J.M. and Parejo, D. 2002. Food selection of wintering common cranes (*Grus grus*) in holm oak (*Quercus ilex*) dehesas in south-west Spain in a rainy season. *Journal of Zoology* 256: 71–79.
- Aviles, J.M. and Bednekoff, P.A. 2007. How do vigilance and feeding by common cranes *Grus grus* depend on age, habitat, and flock size? *Journal of Avian Biology* 38: 690–697.
- Beauchamp, G. 2003. Group-size effects on vigilance: a search for mechanisms. *Behavioural Processes* 63: 141–145.
- Beauchamp, G. 2008: What is the magnitude of the group-size effect on vigilance? *Behavioural Ecology* 19: 1361–1368.
- Borad, C.K., Mukherjee, A. and Parasharya, B.M. 2001. Nest site selection by the Indian sarus crane in the paddy crop agroecosystem. *Biological Conservation* 98: 89–96.
- Caraco, T., Martindale, S. and Pulliam, H.R. 1980. Avian flocking in the presence of a predator. *Nature* 285: 400–401.
- Cimprich, D.A., Woodrey, M.S. and Moore, F.R. 2005. Passerine migrants respond to variation in predation risk during stopover. *Animal Behaviour* 69: 1173–1179.
- Cramp, S. and Simmons, K.E.L. 1980. The Birds of Western Palearctic. Oxford: Oxford Univ. Press, Vol. 2, 695 pp.
- Díaz, M., González, E., Muñoz-Pulidob, R. and Naveso, M.A. 1996. Habitat selection patterns of common cranes *Grus* grus wintering in holm oak *Quercus ilex* dehesas of central Spain: Effects of human management. *Biological Conserva*tion 75: 119–123.
- Dunning, J.B., Danielson, B.J. and Pulliam, H.R. 1992. Ecological processes that affect populations in complex landscapes. *Oikos* 65: 169–175.
- Elgar, M.A. and Catterall, C.P. 1981. Flocking and predator surveillance in house sparrows: test of a hypothesis. *Animal Behaviour* 29: 868–872.
- Elmberg, J., Arzel, C., Gunnarsson, G., Holopainen, S., Nummi, P., Pöysä, H. and Sjöberg, K. 2020. Population changes in breeding boreal waterbirds in a 25-year perspective: What characterises winners and losers? *Freshwater Biolo*gy 65: 167–177.
- Fox, A.D., Elmberg, J., Tombre, I.M. and Hessel, R. 2017. Agriculture and herbivorous waterfowl: A review of the scientific basis for improved management. *Biological Re*views 92: 854–877.

- Fox, A.D. and Madsen, J. 2017. Threatened species to super-abundance: The unexpected international implications of successful goose conservation. *Ambio* 46: 179–187.
- Franco, A.M.A., Brito, J.C. and Almeida, J. 2000 Modelling habitat selection of Common Cranes *Grus grus* wintering in Portugal using multiple logistic regression. *Ibis* 142: 351–358.
- Frid, A. 1997. Vigilance by female Dall's sheep: interactions between predation risk factors. *Animal Behaviour* 53: 199–808.
- Heikkinen, S., Valtonen, M., Härkälä, A., Johansson, H., Harmoinen, J., Helle, I., Mäntyniemi, S. and Kojola, I. 2022. Susikanta Suomessa maaliskuussa 2022: Luonnonvara- ja biotalouden tutkimus 59/2022 [Wolf population in Finland in March 2022: Natural resources and bioeconomy research 59/2022]. Helsinki: Luonnonvarakeskus, 139 pp. (in Finnish with English abstract). URL: http://urn. fi/URN:ISBN:978-952-380-470-8.
- IUCN. 2022. The IUCN Red List of Threatened Species. Version 2022-2. URL: https://www.iucnredlist.org (accessed on 20 July 2023).
- Leito, A., Truu, J., Ounsaar, M., Sepp, K., Kaasik, A., Ojaste, I. and Mägi, E. 2008. The impact of agriculture on autumn staging Eurasian Cranes (*Grus grus*) in Estonia. *Agricultural and Food Science* 17: 53–62.
- Leito, A., Bunce, R.G.H., Külvik, M., Ojaste, I., Raet, J., Villoslada, M., Leivits, M., Kull, A., Kuusemets, V., Kull, T., Metzger, M.J. and Sepp, K. 2015. The potential impacts of changes in ecological networks, land use and climate on the Eurasian crane population in Estonia. *Landscape Ecology* 30: 887–904.
- Lima, S.L. and Dill, L.M. 1990. Behavioral decisions made under the risk of predation: a review and prospectus. *Canadian Journal of Zoology* 68: 619–640.
- Lima, S.L. and Bednekoff, P.A. 1999. Back to the basics of antipredatory vigilance: can nonvigilant animals detest attack? *Animal Behaviour* 58: 537–543.
- Littlefield, C.D. 1995: Sandhill crane nesting habitat, egg predators, and predator history on Malheur National Wildlife Refuge, Oregon. Northwestern Naturalist 76: 137–143.
- Lundin, G. et al. 2005. Cranes where, when and why? A guide book for visitors in European crane areas and ideas how to manage cranes in an agricultural environment Vår Fågelvärld Supplement 43. Stockholm: Swedish Ornithological Society, 228 pp.
- McIvor, D.E. and Conover, M.R. 1994. Impact of greater Sandhill crane foraging on corn and barley crops. *Agriculture*, *Ecosystems and Environment* 49: 233–237.
- McNamara, J.M. and Houston, A.I. 1986. The common currency for behavioral decisions. *American Naturalist* 127: 358–378.
- Montràs-Janer, T., Knape, J., Nilsson, L., Tombre, I., Pärt, T. and Månsson, J. 2019. Relating national levels of crop damage to the abundance of large grazing birds: implications for management. *Journal of Applied Ecology* 56: 2286–2297.
- Moody, A.L., Houston, A.I. and McNamara, J.M. 1996. Ideal free distributions under predation risk. *Behavioral Ecology and Sociobiology* 38: 131–143; https://doi.org/10.1007/ s002650050225.
- Mysterud, A. and Ims, R.A. 1998. Functional responses in habitat use: Availability influences relative use in trade-off situations. *Ecology* 79: 1435–1441.
- Németh, Z. and Moore, F. 2007. Unfamiliar stopover sites and the value of social information during migration. *Journal* of *Ornithology* 148: 369–376.
- Niemi, M., Eronen, V., Aitto-oja, S. and Nummi, P. 2009: Kurkien aiheuttamat viljelysvahingot ja niiden ennaltaehkäisy [Crop damage caused by cranes and its prevention]. Suomen ympäristö 28/2009. Helsinki: Ympäristöministeriö,

62 pp. (in Finnish with English abstract). Available online at: https://helda.helsinki.fi/server/api/core/bitstreams/a90e9b-bc-04c1-469d-b72d-017d78bd9c64/content.

- Nowald, G., Fanke, J. and Hansbauer, M.M. 2018. Linking Crane Life History and Feeding Ecology with Natural Habitats and Agricultural Lands. In: Austin, J.E. Morrison, K.L. and Harris, J.T. (Eds.) Cranes and Agriculture: A Global Guide for Sharing the Landscape. Baraboo, Wisconsin, USA: International Crane Foundation, p. 18–34.
- Pulliam, H.R. 1973: On the advantages of flocking. Journal of Theoretical Biology 38: 419–422.
- R Core Team. 2020. R: A language and environment for statistical computing. Vienna, Austria: R Foundation for Statistical Computing. URL: https://www.R-project.org/.
- Stephens, D.W. 1981. The logic of risk-sensitive foraging preferences. *Animal Behaviour* 29: 628–629.

Supplements

 Table S1.1. Model selection of the binary model for foraging time budget

Models	Model description	AIC values
Full model	Foraging_binary ~ fVegetation +	422.26
(1 st round)	fLocation + fFlock_size_class +	
	Distance_bird + Time + fWeather +	
	(1 fFlock_ID)	
	- fFlock_size_class	419.29
	- fWeather	421.47
	<none></none>	422.26
	- fLocation	423.99
	- Distance_bird	426.66
	- Time	425.96
	- fVegetation	572.19
2 nd round	Foraging_binary ~ fVegetation +	419.29
	fLocation + Time + Distance_bird +	
	fWeather + (1 fFlock_ID)	
	- fWeather	418.31
	<none></none>	419.29
	- fLocation	420.35
	- Time	421.96
	- Distance_bird	423.18
	- fVegetation	569.86
3 rd round	Foraging_binary ~ fVegetation +	418.31
	fLocation + Distance_bird +	
	Time + (1 fFlock_ID)	
	<none></none>	418.31
	- fLocation	419.31
	- Time	420.89
	- Distance_bird	421.39
	- fVegetation	567.86

- Stephens, D.W. and Krebs, J.R. 1986. Foraging theory. New Jersey: Princeton University Press, 247 pp.
- Sugden, L.G., Clark, R.G., Woodsworth, E.J. and Greenwood, H. 1988. Use of cereal fields by foraging Sandhill cranes in Saskatchewan. *Journal of Applied Ecology* 25: 111–124.
- Végvári, Z. 2002. Autumn staging and habitat selection by common cranes *Grus grus* in the Hortobagy National Park, Hungary. *Folia Zoologica* 51: 221–225.
- Ympäristöministeriö. 2019: Luonnonsuojelulailla rauhoitettujen lajien aiheuttamien vahinkojen korvausmenettelyn ja ennaltaehkäisyn lainsäädäntöä valmistelevan hankkeen loppuraportti [Final report of the project preparing legislation for the compensation procedure and prevention of damage caused by species protected by the Nature Conservation Act]. Helsinki: Ympäristöministeriö, 98 pp. (in Finnish).

 Table S1.2. Model selection of the conditional model (Gamma model) of the foraging time budget

incust) of the foraging time cauget				
Models	Model description	AIC values		
Full model	Foraging_positive ~ fVegetation +	1774.71		
(1 st round)	fLocation + fFlock_size_class +			
	Uistance_bird + Time + fWeather +			
	(TIFIOCK_ID)	1760 0		
		1700.0		
		1771 3		
		1771.8		
	- fWeather	1772 9		
		1774 71		
	- fVegetation	1785.6		
2 nd round	Foraging positive \sim fVegetation +	1768.8		
	fLocation + Distance bird + Time +			
	fWeather + (1 fFlock_ID)			
	- Time	1767.1		
	- fLocation	1767.5		
	- Distance_bird	1767.6		
	<none></none>	1768.8		
	- fWeather	1769.0		
	- fVegetation	1780.6		
3 rd round	Foraging_positive ~ fVegetation +	1767.1		
	fLocation + Distance_bird +			
	fl ocation	1765.0		
	- IEOCATION Distance bird	1765.9		
		1767 1		
	- fWeather	1767.3		
	- fVegetation	1779.4		
4 th round	Foraging positive ~ fVegeta-	1765.9		
i iounu	tion + Distance bird + fWeath-	1100.0		
	er + (1 fFlock_ID)			
	- Distance_bird	1764.4		
	<none></none>	1765.9		
	- fWeather	1766.2		
	- fVegetation	1779.6		
5 th round	Foraging_positive ~ fVegetation + fWeather + (1 fFlock ID)	1764.4		
	<none></none>	1764.4		
	- fWeather	1766.0		
	- fVegetation	1777.7		

Models	Model description	AIC values
Full model	Vigilance_binary ~ fVegetation +	178.54
(1 st round)	fLocation + fFlock_size_class +	
	Distance_bird + Time + tWeather +	
	(TITFIOCK_ID)	170.00
	- IFIOCK_SIZE_CIASS	172.29
	- Tvegetation	174.09
	- Ivvealiter	174.04
	- Distance_bird	175.70
	- ILOCALION	175.00
		170.10
and round		170.04
2 nd round	fl ocation + Distance bird + Time +	172.29
	fWeather + (1lfFlock ID)	
	- fVegetation	170.29
	- fWeather	170.43
	- fLocation	171.68
	- Distance bird	171.74
	- Time	172.15
	<none></none>	172.29
3 rd round	Vigilance binary ~ fLocation +	170.29
	Distance_bird + Time + fWeather +	
	(1 fFlock_ID)	
	- fWeather	168.44
	- fLocation	169.68
	- Distance_bird	169.74
	- Time	170.21
	<none></none>	170.29
4 th round	Vigilance_binary ~ fLocation +	168.44
	Distance_bird + Time + (TITFIOCK_ID)	407 70
	- Distance_bird	167.78
		167.82
	- Time	168.32
C th and a l	<none></none>	168.44
5" round	Time + (1 fFlock_ID)	107.78
	- Time	167.38
	<none></none>	167.78
	- fLocation	168.10
6 th round	Vigilance_binary ~ fLocation +	167.38
	(1 TFIOCK_ID)	407 00
	<none></none>	107.38
	- ILocation	108.13

 Table S2.1. Model selection of the binary part for time budget of vigilance

Table S2.2. (continued)

Models	Model description	AIC values
	- fLocation	3423.9
	<none></none>	3423.9
	- Distance_bird	3424.8
	- Time	3426.4
	- fFlock_size_class	3426.9
3 rd round	Vigilance_positive ~ fLocation +	3423.5
	fFlock_size_class + Distance_bird + Time + (1 fFlock_ID)	
	- fLocation	3423.4
	<none></none>	3423.5
	- Distance_bird	3424.7
	- Time	3426.4
	- fFlock_size_class	3426.5
4 th round	Vigilance_positive ~ fFlock_	3423.4
	size_class + Distance_bird +	
	Time + (1 fFlock_ID)	
	<none></none>	3423.4
	- Distance_bird	3423.7
	- Time	3425.9
	- fFlock_size_class	3426.9

 Table S3.1. Model selection of the binary part for time budget for preening

Models	Model description	AIC values
Full model	Preening_binary ~ fVegetation +	445.93
(1 st round)	fLocation + fFlock_size_class +	
	Distance_bird + Time + fWeather +	
	(1 fFlock_ID)	444.00
	- fFlock_size_class	441.83
	- lime	444.47
	- fLocation	445.47
	<none></none>	445.93
	- Distance_bird	449.31
	- fWeather	455.31
	- fVegetation	541.46
2 nd round	Preening_binary ~ fVegetation +	441.83
	fLocation + Distance_bird + Time +	
	fWeather + (1 fFlock_ID)	100.00
	- lime	439.98
	<none></none>	441.83
	- fLocation	442.18
	- Distance_bird	446.30
	- fWeather	451.57
	- fVegetation	537.99
3 rd round	Preening_binary ~ fVegetation +	439.98
	fLocation + Distance_bird +	
	fWeather + (1 fFlock_ID)	
	<none></none>	439.98
	- fLocation	440.21
	- Distance_bird	444.54
	- fWeather	449.65
	- fVegetation	537.73

Table S2.2. Model selection of the conditional model (Gamm	ıa
model) of time budget for vigilance	

Models	Model description	AIC values
Full model	Vigilance_positive ~ fVegetation +	3426.4
(1 st round)	fLocation + fFlock_size_class +	
	Distance_bird + Time + fWeather +	
	(1 fFlock_ID)	
	- fVegetation	3423.9
	- fWeather	3425.5
	- fLocation	3425.9
	<none></none>	3426.4
	- Distance_bird	3426.8
	- Time	3428.4
	- fFlock_size_class	3428.8
2 nd round	Vigilance_positive ~ fLocation +	3423.9
	Distance_bird + Time + fWeather +	
	fFlock_size_class + (1 fFlock_ID)	
	- fWeather	3423.5

Models	Model description	AIC values
Full model	Preening_positive ~ fVegetation +	2497.3
(1 st round)	fLocation + fFlock_size_class +	
	Distance_bird + Time + fWeather +	
	(1 fFlock_ID)	
	- fFlock_size_class	2491.3
	- fWeather	2493.3
	- fLocation	2493.3
	- Distance_bird	2493.6
	- Time	2494.4
	<none></none>	2497.3
	- fVegetation	2502.5
2 nd round	Preening_positive ~ fVegeta-	2491.3
	tion + fLocation + Distance_bird +	
	Time + fiveather + (TITFIOCK_ID)	0.400.4
		2489.4
	- fvveather	2489.4
	- lime	2489.6
	- Distance_bird	2489.9
	<none></none>	2491.3
	- fVegetation	2498.1
3 rd round	Preening_positive ~ fVegetation +	2489.4
	(1)fElock ID)	
	fMoothor	2497 5
	Timo	2407.3
	Distance bird	2407.7
		2400.2
	fl/ogetation	2409.4
4 th round	$\frac{1}{2} = \frac{1}{2} + \frac{1}$	2490.1
4 100110	Distance bird + Time + (1)fElock ID)	2407.5
	- Time	2485 8
	- Distance bird	2486.2
	<none></none>	2487 5
	- fl/egetation	2407.3
5 th round	Preening positive \sim fVegetation +	2485.8
5 Touria	Distance bird + (1lfFlock ID)	2400.0
	- Distance bird	2484 6
	<none></none>	2485.8
	- fVegetation	2494.4
6 th round	Preening positive ~ fVegetation +	2484.6
	(1 fFlock ID)	
	<none></none>	2484.6
	- fVegetation	2493.0

 Table S3.2. Model selection of the conditional model (Gamma model) of time budget for preening

Table S4.1. (continued)

Models	Model description	AIC values
	<none></none>	498.75
	- Distance_bird	499.91
	- Time	500.85
	- fVegetation	518.01
3rd round	Moving_binary ~ fVegetation + Distance	_ 497.58
	bird + fWeather + (1 fFlock_ID)	
	- fWeather	496.22
	<none></none>	497.58
	- Distance_bird	499.26
	- Time	505.12
	- fVegetation	517.50
4 th round	Moving_binary ~ fVegetation +	496.22
	Distance_bird + Time + (1 fFlock_ID)	
	<none></none>	496.22
	- Distance_bird	498.92
	- Time	503.83
	- fVegetation	516.63
	- TVegetation	510.03

 Table S4.2. Model selection of the conditional model (Gamma model) of time budget for moving

,	6 6	
Models	Model description	AIC values
Full model	Moving_positive ~ fVegetation +	1054.2
(1 st round)	fLocation + fFlock_size_class +	
	Distance_bird + Time + fWeather +	
	(TITFIOCK_ID)	1051 0
	- IFIOCK_SIZE_CIASS	1051.0
	- ILOCATION	1055.1
		1053.1
		1053.5
	Chone>	1054.2
	- Distance_bird	1055.0
and round	- Ivegetation	1074.7
Zina round	fl ocation + Distance bird + Time +	1051.6
	fWeather + (1 fFlock ID)	
	- fLocation	1049.8
	- Time	1049.9
	- fWeather	1050.1
	<none></none>	1051.8
	- Distance bird	1051.8
	- fVegetation	1071.4
3 rd round	Moving_positive ~ fVegetation +	1049.78
	fLocation + Distance_bird +	
	fWeather + (1 fFlock_ID)	
	- Time	1047.9
	- fWeather	1048.1
	<none></none>	1049.78
	- Distance_bird	1049.8
	- fVegetation	1069.6
4 th round	Moving_positive ~ fVegetation +	1047.9
	Distance_bird + fVveather + (1 fFlock_ID)	1010.0
		1046.2
	- Distance_bird	1047.9
	<none></none>	1047.9
Eth. I	- Tvegetation	1068.1
5 th round	Moving_positive ~ 1 Vegetation + Distance bird + (1 fFlock ID)	1046.2
	- Distance bird	1045.9
	<none></none>	1046.2
	- fVegetation	1067.0
6 th round	Moving_positive ~ fVegetation +	1045.9
	(1 fFlock_ID)	
	<none></none>	1045.9
	- fVegetation	1069.7

Table S4.1. N	Model	selection	of the	binary	part f	for t	ime	bud	get
for moving									

Models	Model description	AIC values
Full model (1 st round)	Moving_binary ~ fVegetation + fLocation + fFlock_size_class + Distance_bird + Time + fWeat- her + (1)fFlock_ID)	501.97
	- fLocation	498.75
	- fFlock_size_class	499.02
	- fWeather	499.76
	- Distance_bird	500.77
	<none></none>	501.97
	- Time	502.09
	- fVegetation	519.76
2 nd round	Moving_binary ~ fVegetation + fFlock_size_class + Distance_bird + fWeather + (1 fFlock_ID)	498.75
	- fFlock_size_class	497.58
	- fWeather	498.24