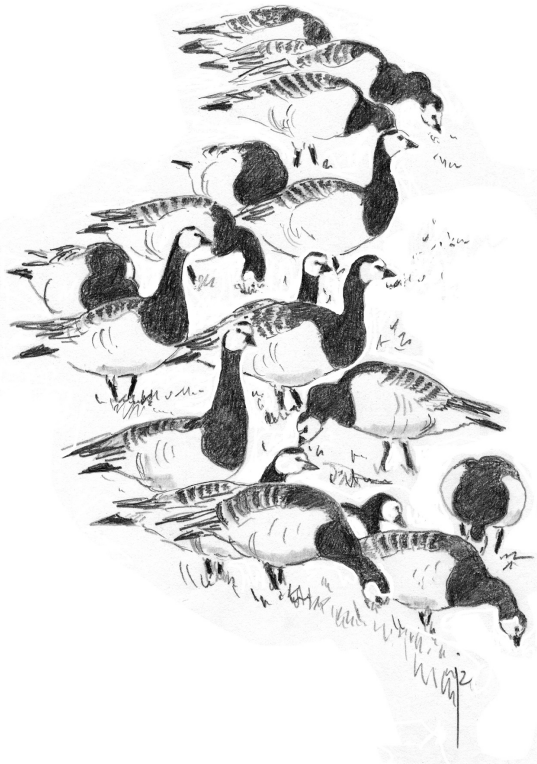


Social information use by Barnacle Geese *Branta leucopsis*, an experiment revisited

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Reproducing research results is one of the cornerstones of science. However, few biological findings are actually replicated. Here, we repeat a study done more than 35 years ago on social information use in Barnacle Geese. In the original study, models of Barnacle Geese were used to measure how they attracted wild Barnacle Geese (Drent & Swierstra 1977). Models were placed in different locations in a pasture and these models attracted many wild Barnacle Geese, providing strong evidence for the use of social information. 37 years later we repeated this experiment, using the same models, the same area and a similar research protocol. Despite an abundance of wild Barnacle Geese in the area frequently flying over the models, the models did not elicit a landing response. In line with the original study, we scored vigilance rates and abundance of geese. Comparing these data to previous records we found that total abundance increased but that vigilance rates were lower than previously recorded. The decreased vigilance suggests that the landscape has become safer or that competition between geese has intensified; both could explain a reduced use of social information. More generally, our study shows the importance of repeating experiments in ecology, especially in a rapidly changing world.

Key words: Barnacle Geese, foraging, social information use, reproducibility

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The reproducibility of scientific findings is one of the pillars of knowledge acquisition and the scientific approach. Reproducibility is what sets science apart from anecdotes (Russell 2013). Similar outcomes obtained by independent researchers are considered the scientific gold standard (Jasny *et al.* 2011). However, the actual repetition of previous studies rarely occurs. Funding bodies usually explicitly request that research is novel and replicated studies are notoriously hard to get published providing a strong incentive for developing novel research questions rather than replicating previous findings. This has led to a climate in which the repetition of previous work is scarcely done (Russell 2013). This is problematic since there are numerous ways whereby researchers can arrive at the wrong

conclusions (Ioannidis 2005). An independent study, verifying or falsifying earlier research outcomes can be a powerful protective mechanism. In ecology, there is the additional effect of a rapidly changing world, which can lead to different research outcomes. More recently there is an increasing awareness of the importance of reproducibility. Leading journals have started to facilitate reproducibility of studies (e.g. by requesting enclosure of the exact methodological details; Announcement 2013) and new initiatives like the 'Reproducibility Initiative' are funded with the explicit goal of reproducing previous research outcomes. Nonetheless, repetition of previous work is scarce and the field of ecology is no exception to this.

Here we repeated an experiment done more than

35 years ago on Barnacle Geese *Branta leucopsis* on the island Schiermonnikoog, The Netherlands (Drent & Swierstra 1977). This study investigated the effect of model geese (decoys) in a pasture on attracting wild Barnacle Geese and thus investigated the use of social information. Individuals can use two different sources of information. They can either gather personal information by interacting with the physical environment on a trial-and-error basis or they can use social information by observing others individuals (Danchin *et al.* 2004). Social information can either be based on signals, specifically developed to transmit information or by cues provided unintentionally by other individuals (inadvertent social information; Danchin *et al.* 2004). Social animals, animals which interact intensively with other members of its species, observe other individuals to learn from them where, what and how to eat (Galef & Giraldeau 2001). The use of social information has been demonstrated in a wide variety of species (Galef & Giraldeau 2001, Danchin *et al.* 2004, Valone 2007) and is known to affect various important aspects of an individual's ecology, such as foraging, dispersal and space use (Seppanen *et al.* 2007). Individuals can adaptively change the type of information they rely on, for example in response to changes in costs and benefits of collecting personal and social information (Templeton & Giraldeau 1995, 1996, Valone 2007, Webster & Laland 2008). Likewise, the type of information individuals use depend on the reliability of the information (van Bergen *et al.* 2004). Closely related species can differ in social information use (Coolen *et al.* 2003), and within the same species there can be inter-individual differences in social information use due to personality differences (Kurvers *et al.* 2010b). The use of social information might thus differ between individuals, between species, but also between contexts and therefore it is by no means a given that previous outcomes on social information use are still valid.

The original study (Drent & Swierstra 1977) is a classic example of social information use. The authors placed a group of models in different locations in a pasture and studied how this affected the habitat choice of wild Barnacle Geese that flew over searching for suitable foraging habitats. The authors found that model geese elicited a strong landing response in wild Barnacle Geese. When model geese were present in a pasture, there were many more landings of wild geese in that area than without the model geese present (see Zhu *et al.* (1987) for similar findings in Barnacle Geese and Inglis & Isaacson (1978) for Dark-bellied Brent Geese *Branta bernicla bernicla*). 37 years later we

repeated this experiment using the same goose models in the same area and at the same time of year. The research took place in the polder of the island Schiermonnikoog, The Netherlands. The polder is still dominated by the same grass species *Lolium perenne* and *Poa pratensis* as in the 1970s although the individual fields now are larger. These grass species are the main diet of Barnacle Geese grazing in the polder of Schiermonnikoog (Ebbinge *et al.* 1975, Ydenberg & Prins 1981).

Following the original study, we placed the same goose models in different locations in the same polder, which is still used by wild Barnacle Geese every winter since the original experiment and studied their effect on landings of wild Barnacle Geese. In line with the original study, we also collected data on grass height, a prime determinant of habitat use in the species (e.g. Si *et al.* 2011), vigilance behaviour and total geese abundance.

METHODS

In the winter of 2010/2011, we exposed wild Barnacle Geese to groups of model geese, following closely the procedures as described in the original study (Drent & Swierstra 1977). We used the same models (decoys) as the ones from 1973–1974. These models were made of fibreglass painted black, grey and white, identical to wild Barnacle Geese. The models had been stored dark and dry at the former Zoological Laboratory in Haren, The Netherlands. Visual inspection of the models and old colour photographs showed that they looked very much like 37 years ago. Two body postures were used in the experiment: 'alert' (head up with neck stretched) and 'grazing' (head down as if grazing; Figure 1).

The models were mounted in the ground by metal wire legs which could be bent to place the decoys in the realistic postures. As in the original study, we placed the decoy flock out in a polder pasture around sunset the day before the experiment when the wild geese were away to roost on the mudflats. To imitate a natural situation, we placed the model geese in a circular flock with their heads turned into the wind. Alert model geese were placed in the back of the flock. These placement properties were derived from observations of wild Barnacle Geese flocks foraging on the polder pastures of Schiermonnikoog. We used 36 model geese, 32 in the grazing posture and 4 in the alert posture, which corresponds to the largest flock size used by Drent & Swierstra (1977). The research area in which we placed the models was a large rectangular pasture of 700 by 200 meters in the eastern part of the polder



Figure 1. Group of model Barnacle Geese. The two distinct body postures, ‘alert’ and ‘grazing’, can be clearly distinguished. Schiermonnikoog, 15 February 2011.

(53°28'39"N, 6°12'21"E) close to the location used by Drent and Swierstra (53°28'30"N, 6°10'25"E). Before starting the experiment, we did daily observations and dropping counts to verify and confirm that our research area was regularly visited by wild Barnacle Geese. We divided the research area into 14 similar sized plots of one hectare each. The plots were marked with small aluminium poles. The evening before the first day of the experiment, the decoy flock was placed in the middle of a randomly chosen plot. The decoy flock was present in a specific plot for two days before moving them to another, randomly chosen without replacement, plot to avoid possible plot preferences by wild Barnacle Geese. Weekend observations were excluded to avoid habituation of the wild geese to the decoys and to minimize disturbances by members of the public (recreation pressure is highest during weekends).

Observations were done by telescope from a camouflaged shelter placed on the edge of the research area. For 2 months (18 November 2010 – 12 January 2011), the morning flights of Barnacle Geese were recorded. During these morning flights, geese leave their roost on

the mudflats outside the embanked polder, and fly into the polder pastures to search for suitable foraging grounds (Ydenberg *et al.* 1983). Following the original study, we scored each morning which of the 14 plots was the first to be visited by geese (‘first landing’) and we counted the number and size of flocks flying within visible range of the models, defined as flying either over the research area or at an estimated maximum of 200 m from the research area. Further, starting at 9:00 h and ending at 13:00 h, we did hourly counts. During these counts we recorded for each plot whether geese were present or absent, and if present the total number of geese present in each of the 14 research plots. During these counts we also measured vigilance behaviour of each flock present in the research area by recording the number of alert birds and the total number of birds per flock ($n = 77$ flocks). We also regularly counted the total number of Barnacle Geese in the entire polder (c. 260 ha) for comparison to older records. Last, because Barnacle Geese may use grass height as selection criterion to land or not (Vickery & Gill 1999; Heuermann *et al.* 2011; Si *et al.* 2011), we determined grass heights

in all the 14 plots using a disc pasture meter. We walked transects along the longest side of the pasture and measured grass height every 20 meters, starting 10 meters from the field edge (18 measurements per research plot).

Statistical analysis

To study whether the models significantly affected the number of 'first landings', we compared the 'observed first landings' in the plot with the decoys and in the remaining 13 plots with the 'expected first landings' using a chi-square test. As expected values we assumed that for each landing in the plot containing the decoys there would be 13 landings in other plots. To study whether the models significantly affected the presence of geese in the plots, we compared the 'observed presence of geese (y/n)' during the hourly counts in the plot with the decoys and in the remaining 13 other plots with the 'expected presence of geese (y/n)' using a chi-square test. Again, with the expectation that for each flock present in the plot containing the decoys there would be 13 flocks present in the other plots. Last, to compare differences in grass height measurements between the 14 research plots we performed a Kruskal-Wallis test.

RESULTS

The daily total number of Barnacle Geese counted during the winter of 2010/2011 in the 260 ha polder on Schiermonnikoog ranged between 4200 and 6900. On our 15 experimental days, a daily average of 1287 individual geese distributed over 22 flocks flew over our experimental decoys on their morning flight into the polder. The number of flocks per day ranged from 7 to 41 and flock size ranged from 1 to 2000 individuals. These observations match those reported by Ydenberg *et al.* (1983), who described in detail the morning flight of Barnacle Geese on Schiermonnikoog. There were no significant differences in grass height between the plots ($H = 11.78$, $df = 13$, $P > 0.5$; range: 2.95–3.48 cm) excluding any preference for Barnacle Geese following vegetation height.

Of the first (i.e. no other geese yet present) flock to land in our research area on each of the 15 experimental days, two (13.3%) occurred in the plot with decoys and 13 in one of the remaining 13 plots. This is not significantly different from a random expectation ($\chi^2 = 0.58$, $df = 1$, $P = 0.45$). In total we counted 77 flocks in our research area during the hourly counts. Ten of these flocks were in the field with the decoys and 67 were

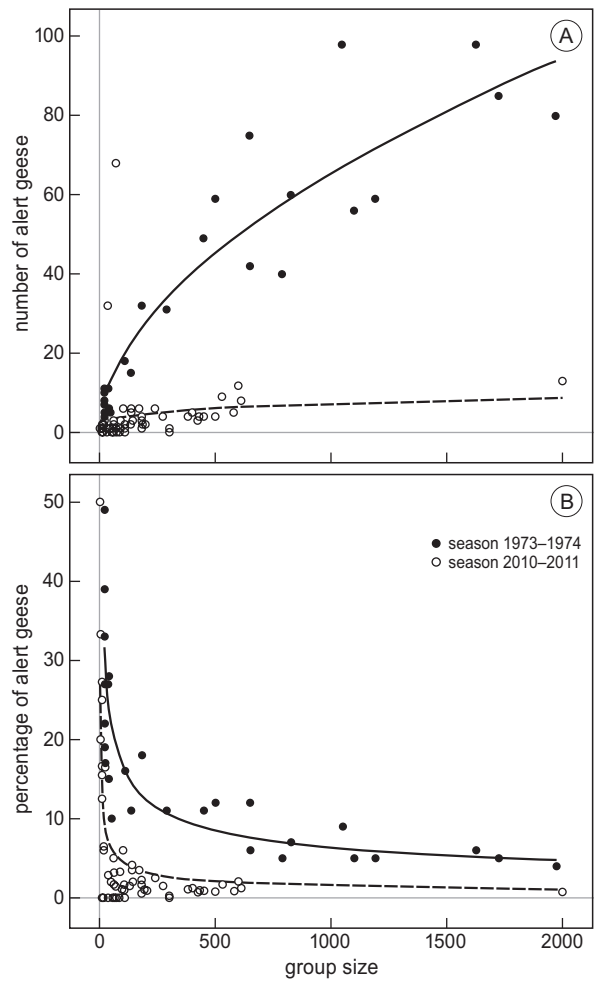


Figure 2. (A) The total number of alert geese and (B) the percentage of alert geese as a function of group size during the winter of 2010/2011 (open circles and dashed line), and during the winter of 1973/1974 (closed circles, solid line). Lines are fitted exponential curves. In both seasons, (A) the total number of alert geese increases exponentially with increasing group size and (B) the percentage of alert geese decreases exponentially with group size. In 2010/2011 the total number of alert individuals and the percentage of alert geese are significantly lower than in 1973/1974.

in the remaining 13 plots, which is not significantly different from random expectation ($\chi^2 = 3.09$, $df = 1$, $P = 0.08$).

Figure 2 shows the relationship between group size and vigilance. As expected, the number of alert geese increases with group size (Figure 2A), while the percentage of alert geese decreases with group size (Figure 2B).

We compare our observations with those made by Drent & Swierstra (1977) in Table 1. Drent & Swierstra

(1977) reported a strong effect of the decoys on ‘first landings’ with 19 out of 22 first landings in the same plot as the models, and only 3 first landings in the remaining part of the research area which is approximately 15 fold the size of the plot containing the models. In sharp contrast, we only observed 2 out of 15 first landings in the same plot as the models and 13 out of 15 first landings in the remaining part of the research area, which is 13 fold the size of the plot containing the models (Figure 3). Moreover, vigilance levels are lower than the observations of Drent & Swierstra (1977; Figures 2A, B). To illustrate, we fitted exponential curves through the data on group size and number of alert birds (Figure 2A) and calculated the expected number of alert birds for a group size of 500 for both years. In 1973 the estimated number of alert geese is 44 for a group size of 500, whereas in 2010 this number is estimated to be only 6.

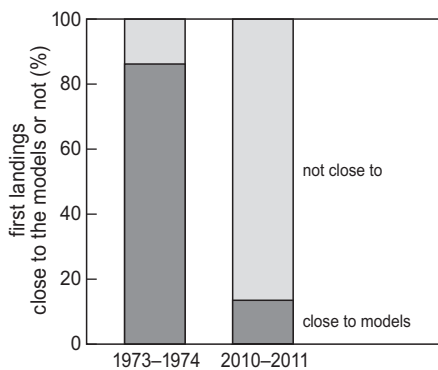


Figure 3. The percentage of first landings close to the models (dark bars), and the percentage of first landings away from the models (white bars). In the winter of 1973/1974, most of the first landings (86.4%) occurred close to the models, indicative of social information use. In the winter of 2010/2011 few landings (13.3%) occurred close to the models and the probability of first landing did not differ from random expectation.

Table 1. A comparison between the observations made here (winter 2010/11) and those made by Drent & Swierstra (1977) in 1973/74 on the attraction of Barnacle Geese to decoys during the morning post-roosting flight into the polder on Schiermonnikoog. The vigilance level is estimated as the number of alert birds in a flock of 500, as estimated from the fitted exponential curves (see Figure 2A).

Winter	1973/74	2010/2011
Number of observation days	22	15
Number of geese on island	3000–4000	4200–6900
First landings	19/22	2/15
Vigilance level	44	6

DISCUSSION

The attractiveness of the model geese has substantially changed over the years. We had few landings of wild geese near our model flocks during their morning flights, even though we used exactly the same model geese on the same location as in the original experiment. Our results are clearly different from the results of the Drent and Swierstra experiment, with only two out of fifteen ‘first landings’ in our experiment compared to the 19 out of 22 ‘first landings’ in the Drent & Swierstra experiment. Our research area was, however, still frequently visited by wild Barnacle Geese as evidenced by the number of geese flying over and landing. Also, the geese still roost on the same mudflats and leave the mudflats shortly before sunrise, flying over the sea-dyke to land in the pastures in the polder as they did 35 years ago (Ydenberg *et al.* 1983). Thus, while there are no apparent changes in the daily routines of Barnacle Geese at Schiermonnikoog, our results strongly suggest that Barnacle Geese do not currently rely as strongly on social information as they did in the 1970s. We provide three non-mutually exclusive explanations.

First, it is possible that the vegetation in the polder pasture is more homogenous than in the 1970s. The value of social information is higher in heterogeneous landscapes when there are large differences in food quality/quantity between patches. If there are little differences between food patches and intake rates are not different between patches then the value of social information of food opportunities is low, since each foraging decision gives the same return. Geese select foraging areas primarily on nitrogen content and sward height (Riddington *et al.* 1997, Hassall & Lane 2001, Durant *et al.* 2004, Bos *et al.* 2005, van der Graaf *et al.* 2006, Si *et al.* 2011). The pastures at Schiermonnikoog are currently heavily fertilized and the food quality is so high that even in winter all areas provide good foraging habitat for Barnacle Geese. Also, there were no differences in grass length between the plots in our research area, and the grass length was close to the optimal grass length of 3 to 4 cm (Heuermann *et al.* 2011). So the absence or presence of geese (as imitated by the decoys) in the polder of Schiermonnikoog is not likely to provide useful information about the quality of food. We could not find information about fertilisation regimes in the 1970s in the polder, but species composition was the same as at present (T. Talsma pers. comm.); in the early 1980s grass quality was already above maintenance requirements of the geese (Prins & Ydenberg 1985). It is thus not unlikely that even in the mid-1970s the presence of geese did not indicate ‘good

food'. Support for this interpretation comes from additional observations we made. In February and March 2011, we placed our decoys on the adjacent salt marshes that Barnacle Geese use as foraging grounds during this time of year (Prins & Ydenberg 1985, Bos & Stahl 2003). In these salt marshes grass quality and quantity is more spatially heterogeneous (Prins & Ydenberg 1985; Bos & Stahl 2003) but in this heterogeneous habitat the decoys also had no effect on goose landings (data not shown). What then is the information the decoys, or in reality, the presence of geese, are conveying to overflying geese? If it is not about food, then perhaps the social information is about safety.

In The Netherlands safety has increased in the last 40 years, partly because of hunting restrictions (Ebbing 1991). As a consequence, Barnacle Geese numbers have increased dramatically over the last decades (Ganter *et al.* 1999; Koffijberg & Günther 2005) and are now estimated to be close to one million birds (Sovon 2014). When Drent and Swierstra started their research, Barnacle Geese were considered so rare and threatened that conducting research on them was rarely allowed (pers. comm. the late G.P. Baerends and the late R.H. Drent). We postulate that in the 1970s geese interpreted the decoys in the fields as indicative of safe conditions for landing. Now that Schiermonnikoog is safer (hunting is banned), the decoys no longer provide any additional information. Support for this hypothesis also comes from the data on the lower vigilance levels we recorded as compared to the 1970s. We found a decline in individual vigilance rate with group size. This is a well-described effect in many species (Pulliam 1973, Elgar 1989, Lima & Dill 1990, Roberts 1996) and is thought to be a consequence of decreased predation risk in larger groups by increased predator detection ('many eyes effect') and a higher dilution of risk (Roberts 1996). Drent and Swierstra found the same pattern in the 1970s. However, overall vigilance rates are lower now than they were in the 1970s (Figure 2). The lower vigilance levels could indicate that geese perceive their environment as safer now. So if safety is less of a concern to geese, then it is expected that this will also decrease their use of social information and flocking. However, vigilance can serve different functions, and a decline in vigilance rates in larger groups is also hypothesized to be a result of increased foraging competition in larger groups (Elgar 1989, Beauchamp 2003) leading to our third and last explanation.

Barnacle Geese indeed suffer from intra-specific competition while foraging, both through direct competitive interactions (i.e. interference competition;

Stahl *et al.* 2001, Kurvers *et al.* 2010a, Kurvers *et al.* 2012) as well as through resource depletion (i.e. exploitative competition; Rowcliffe *et al.* 2004). The number of Barnacle Geese we estimated (4200–6900) are substantially higher than the number of Barnacle Geese in the 1970s (3000–4000; Ydenberg *et al.* 1983) reflecting the general trend of rising numbers of Barnacle Geese in Western Europe (Ganter *et al.* 1999, Eichhorn *et al.* 2009). This increase in abundance could have led to increased intra-specific competition for food. Increased food competition in Barnacle Geese has been suggested to be a driver of several recent behavioural changes in this species, including increased natal dispersal (Forslund & Larsson 1991) and changes in migratory strategies (Eichhorn *et al.* 2009). An increase in food competition is thus a third factor which could explain the reduced vigilance rates, and the reduced use of social information.

As noted by Ryan (2011), true replication under natural conditions is challenging. We attempted to replicate the original study as closely as possible, using the same models, the same experimental set-up and the same fields. However, we still arrived at a different research outcome. That does not mean that the previous observations were invalid and one should be careful of rejecting previous research outcomes (Bissell 2013); it is highly likely that their conclusions about how the world is organized and how geese operate are no longer true. Thus, though we do not reject the conclusions of Drent & Swierstra (1977), we have, by all means and in a Popperian sense, falsified the hypothesis that geese use social information as they used to do. This is rarely done in ecology, but we can now state that Barnacle Geese do not always react to decoys and that decoys do not always provide social information: under some circumstances they do but under other circumstances they do not. This suggests that scientists cannot merely quote a source as if something is 'still' true after many years. The original interpretation loses salience as theory develops further, but the 'facts' can still be quoted even though the 'old facts' have to be placed in a new context.

To conclude, despite frequent fly overs of geese and an abundance of geese in the area, the models did not attract wild Barnacle Geese, in sharp contrast to 37 years ago. Moreover, comparing vigilance rates back then and now, we found a significant reduction in current vigilance rates, suggesting the landscape has become safer or that food competition has intensified. Our study shows the importance of repeating experiments in ecology and treating previous research outcomes with great care.

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SAMENVATTING

Herhaalbaarheid van onderzoek is een van de belangrijkste steunpilaren van de wetenschap. Er is doorgaans echter een sterke drang om vernieuwend onderzoek uit te voeren, omdat het moeilijk is om financiering te vinden voor herhaling van al eerder uitgevoerd onderzoek. Dit heeft geleid tot een situatie in de ecologie waarbij eerder behaalde onderzoeksresultaten vrijwel nooit worden getoetst door het eerder verrichte onderzoek nog eens opnieuw uit te voeren. Hier hebben we een eerder verricht onderzoek naar sociaal informatiegebruik bij de Brandgans *Branta leucopsis* herhaald dat meer dan 35 jaar geleden is uitgevoerd. In de oorspronkelijke studie werden groepen modellen van de Brandgans in de polder van Schiermonnikoog geplaatst om te onderzoeken hoe deze modellen de landingen van wilde Brandgans beïnvloedden. De eerdere studie toonde aan dat de modellen een sterke aantrekkingskracht hadden op de Brandgans. Wij hebben dit onderzoek 37 jaar later met dezelfde modellen en een vergelijkbare onderzoeksopzet in hetzelfde studiegebied herhaald. Ondanks dat de ganzen nog steeds dezelfde vliegbewegingen maken als in de jaren zeventig van de vorige eeuw en in groten getale over de modellen heen vlogen, hadden de modellen geen aantrekkingskracht meer op de wilde ganzen. Ook hebben we gegevens verzameld over de waakzaamheid van de ganzen en de populatieaantallen, en deze vergeleken met de gegevens uit de jaren zeventig. In vergelijking met die periode is het aantal Brandgans op Schiermonnikoog toegenomen en de waakzaamheid van de ganzen drastisch afgenomen. Dit suggereert dat de omgeving veiliger is geworden of dat de competitie tussen de Brandgans is toegenomen. Beide factoren kunnen de vermindering van het gebruik van sociale informatie verklaren. Onze resultaten tonen het belang aan van het herhalen van ecologisch onderzoek en laten zien dat, indien nieuwe resultaten anders zijn, conclusies uit eerder onderzoek dienen te worden bijgesteld.

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