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ORIGINAL ARTICLE

Seasonal differences in at-sea activity of seabirds underline high energetic demands during the breeding period

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Abstract We assessed seasonal differences in at-sea activity of Lesser Black-backed Gulls *Larus fuscus*, Black-legged Kittiwakes *Rissa tridactyla* and Common Guillemots *Uria aalge* in the south-eastern North Sea. The three species correspond to different ecological groups, with Lesser Black-backed Gulls representing omnivorous generalists, Kittiwakes representing surface-feeding pelagic seabirds, and Guillemots representing pursuit-diving pelagic seabirds. Using data from aerial surveys, we differentiated between active (flying or scavenging at fishing vessels) and inactive behaviour (swimming). We estimated the activity budgets of all three species for the different seasons and tested for differences in activity between different seasons. All species exhibited significant seasonal differences in activity, with the highest levels of activity observed during the breeding season. Numbers of flying auks were, however, exceptionally low in autumn due to moult and guarding of not-yet fledged chicks at sea. Our results underline the high energetic demands of the breeding season that lead to increased foraging and travelling activity.

Keywords Black-legged Kittiwake · Lesser Black-backed Gull · Common Guillemot · At-sea activity · Time–activity budget · Seasonality

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Introduction

Activity budgets, in combination with knowledge of energetic costs, provide information on resource allocation of seabirds (Goldstein 1990). They may thus be used as indicators of food availability (Cairns 1987), and provide a basis for ecological energetics models (Tasker and Furness 1996). However, information on activity of seabirds at sea is still scarce, even though the sea represents the major feeding habitat for seabirds and their exclusive habitat outside the breeding season. Data logger studies have started to fill this gap in our knowledge (e.g. Benvenuti et al. 2001; Garthe et al. 2003; Ropert-Coudert et al. 2004), but sample sizes are usually low, and studies have so far mostly covered temporally restricted periods at the order of hours or days. In addition, both interannual variability of extrinsic parameters and individual differences may significantly influence the level of reproductive costs in the breeding season, and thus necessitate multiyear comparisons (Golet and Irons 1999). Moreover, logger studies mostly deal with breeding birds, due to the need to recapture the birds to detach the loggers. Due to technological constraints, few studies focussing on activity of birds have taken place during the non-breeding season (e.g. Daunt et al. 2006; see "Outlook"). Bioenergetics models covering the whole year generally extrapolate from data on breeding birds, and are thus likely to overestimate the energy requirements of seabirds (Ellis and Gabrielsen 2002). Hence, data on seabird activity both during and outside the breeding season are needed to minimise errors in bioenergetics models.

So far, data on seabird occurrence and behaviour collected during surveys at sea have seldom been used to gain information on activity of seabirds (but see Camphuysen 1998), although at-sea surveys of seabird abundance have been carried out in many sea areas around the world, and studies often cover several decades. In the south-eastern North Sea, the German Bight, Seabirds at Sea surveys have been carried out by ship since 1990 and by aircraft since 2002 (Garthe et al. 2007). Data from aerial surveys are more homogeneous with respect to spatial and temporal effort than ship-based surveys, and were thus chosen for the following analyses. Surveys took place throughout the year, and seabird activity was recorded by at least differentiating between swimming and flying behaviour.

Our study aims to assess reasonable indications of the time–activity budgets of selected species during each season in the study area. The null hypothesis implies no differences in activity level between different seasons. However, we expect elevated activity levels of breeding birds during the breeding season, as parent birds need to maintain self-provisioning and must also raise their young by commuting between the colony and often remote foraging areas at sea (Ricklefs 1984).

We formulate the following specific hypotheses:

1. Due to the high energetic demands of individuals during the breeding season, we expect a higher amount of actively foraging or travelling birds during the breeding season compared to the other seasons.
2. Differences in flight activity are expected to be less pronounced in diving species like alcids, as the flight activity observed may not represent activity related to foraging as well. In addition, swimming behaviour includes low proportions of resting (Tremblay et al. 2003). Thus, foraging activity cannot be expressed by considering the behaviour "flying". Nevertheless, the proportion of flying behaviour should be higher due to breeding birds commuting to and from the colony.

Materials and methods

Studies were carried out in the German Bight, which is defined here as the area between 53°21′ and 55°01′N and 05° to 09°E in the south-eastern North Sea. Only species that breed in the study area and forage virtually exclusively at sea were considered appropriate for the analyses. Northern Gannet *Sula bassana*, Northern Fulmar *Fulmarus glacialis* and Razorbill *Alca torda* all meet these criteria, but they are either very scarce or their breeding populations comprise an insignificant share of the total numbers in summer in the German Bight due to large numbers of non-breeding individuals (following Garthe et al. 2007, and breeding numbers given by Dierschke et al. 2007). Thus, only the Lesser Black-backed Gull *Larus fuscus*, the Common Guillemot *Uria aalge* (hereafter "Guillemot") and the Black-legged Kittiwake *Rissa tridactyla* (hereafter "Kittiwake"), whose breeding populations comprised two-thirds or more of their total summer populations, respectively (following Garthe et al. 2007, and breeding numbers given by Koffijberg et al. 2006 and Dierschke et al. 2007), were considered appropriate for the study. While the latter two occupy a single breeding colony on the small offshore island of Heligoland in the study area, Lesser Black-backed Gulls breed in several large colonies along the coast line. During winter, spring and autumn, the proportions of German breeding birds of Kittiwakes and Lesser Black-backed Gulls correspond to 90% or more of the total populations of the two species in the German EEZ of the North Sea (following Garthe et al. 2007, and breeding numbers given by Koffijberg et al. 2006 and Dierschke et al. 2007). In contrast, the majority of the Guillemots observed outside the breeding season belong to populations other than the German breeding population (most probably to the Scottish breeding population). However, the latter do not exhibit different phenologies (compare Grunsky-Schöneberg 1998 and Forrester et al. 2007), and so are not expected to bias our results on activity patterns. The three species correspond to different ecological groups, with Lesser Black-backed Gulls representing omnivorous generalists, Kittiwakes representing surface-feeding pelagic seabirds, and Guillemots representing pursuit-diving pelagic seabirds.

Since 2002, data on seabird occurrence in the German Bight have been recorded by aerial surveys, following the standardised methods described by Kahlert et al. (2000) and Diederichs et al. (2002). Surveys were performed from a high-winged twin-engine Partenavia P-68 provided with bubble windows at a flight altitude of 78 m (250 feet) and a cruising speed of circa 185 km/h (100 knots). The occurrence of birds was recorded within 397 m wide transects running in parallel to the flight route of the observation platform. Under good observation conditions, both sides of the flight route can be covered by two trained observers, resulting in a survey transect of 794 m. All bird sightings were recorded to the second, providing details on species, number, and activity. Survey methods included the recording of information on vessel association of species feeding on fishery discards and offal. The surveys sampled a total area of circa 24,600 km^2, with large sampling areas covered during single surveys. Surveys were mostly restricted to the late morning and noon (Table 1).

Due to inferior observation and identification conditions during aerial surveys, it is not possible to identify age classes on the basis of plumage. By applying the ratios of individuals in adult plumage to individuals in immature plumage recorded in ship-based surveys (85:15% for Lesser Black-backed Gulls and 92:8% for kittiwakes during the respective breeding seasons; German Seabirds at Sea database ship v5.07) to aerial surveys, the results for all birds in aerial surveys can be assumed to mirror the

Table 1 Seasonal survey efforts and main daytime periods sampled by aerial surveys (2002–2006, German Seabirds at Sea database plane v5.06) in the German Bight

Season	Mean area surveyed/year (km^2) ± SD	Earliest start time (UTC)	Latest stop time (UTC)	Main time of day sampled (UTC) (>80% of area surveyed)
Winter	1,265 ± 868	08:46	16:13	10–13
Spring	2,071 ± 1,126	06:39	17:54	8–14
Summer	893 ± 1,718	07:04	13:25	8–11
Autumn	690 ± 552	06:15	14:59	7–11

Classification of seasons as defined for Black-legged Kittiwakes (see Table 2). Total area surveyed = 24,595 km^2

SD, standard deviation

situation of adult birds, and thus mostly involve breeding individuals of both species. However, note that birds in immature plumage comprise first-year and second-year individuals of Kittiwakes and first-year to fourth-year individuals of Lesser Black-backed Gulls, respectively. The mean age of first breeding is 4–5 years in Black-legged Kittiwakes (Glutz von Blotzheim and Bauer 1999; Rothery et al. 2002). Thus, some of the birds identified as being in adult plumage possibly comprise a substantial proportion of the not-yet-breeding immatures. Immature Guillemots can be identified at sea due to their smaller size only in their first weeks at sea after leaving the colony but cannot be identified properly once they are fully grown (proportion of Guillemots identified as immature in summer: 3%; autumn: 16%; winter and spring: <1%; German Seabirds at Sea database ship v5.07). Due to identification difficulties during aerial surveys, we combined data on Guillemot, Razorbill *Alca torda* and "razormot" (Common Guillemot/Razorbill) to obtain an indication of the activity budgets of Guillemots. This group is termed "razormots" in the following text. We considered this method appropriate as breeding numbers of Razorbills at Heligoland are very low compared to the numbers of Guillemots (18 compared to 2,655 apparently occupied nests in 2006; Dierschke et al. 2007). The number of Razorbills corresponds to less than 5% of the number of Guillemots in the German North Sea during spring, summer and autumn. During winter the number of Razorbills corresponds to about 23% of the number of Guillemots (Garthe et al. 2007). However, we assumed that the activity budgets of wintering Razorbills and Guillemots do not differ significantly, and we are therefore confident that the combined data set produces representative results for the Guillemot population of the study area. During rough sea conditions, a flying bird is detected more easily than a swimming bird. This fact influences the results for the estimated time budgets. To compensate for the inconspicuousness of swimming auks at sea, especially during rough conditions, we thus only included data taken under relatively calm conditions (sea state <4).

We assessed the activities of the selected species during all four seasons by distinguishing between flying and swimming individuals and between individuals that were and were not associated with vessels. To interpret our results, we took the proportion of individuals exhibiting a specific behaviour to be an indicator of the proportion of time spent with this behaviour by the respective species in the studied season in order to get an indication of time–activity budgets (instantaneous sampling; Altmann 1974). We considered flying behaviour and vessel association to be active (foraging) behaviour. This classification is appropriate in particular for seabirds that mainly forage at the sea surface, like gulls and terns, and mostly sit on the water surface during resting. Seasons were classified for each species according to breeding, moulting and migration times (Table 2). We assessed the ratio of flying and swimming individuals for each season, year and species. Lesser Black-backed Gulls are frequently associated with

Table 2 Classification of species-specific seasons for the analysis of activity

	Winter	Spring	Summer	Autumn
Lesser Black-backed Gull	01/11/–15/03/	16/03/–15/05/	16/05/–15/07/	16/07/–31/10/
Black-legged Kittiwake	01/11/–29/02/	01/03/–15/05/	16/05/–31/07/	01/08/–31/10/
Common Guillemot	01/10/–29/02/	01/03/–15/04/	16/04/–15/07/	16/07/–30/09/

Spring covers the return to the breeding site and egg laying, while summer comprises the incubation and chick-rearing period in all three species (Prüter 1989; Maul 1994; Grunsky-Schöneberg 1998; Glutz von Blotzheim and Bauer 1999) fishing vessels, feeding on discards and offal. Scavengers at the stern are mostly recorded swimming (pers. observation). We consequently incorporated information on vessel association of single individuals into our analyses of Lesser Black-backed Gulls to test for an influence of vessel association on activity too. Moreover, this method allowed us to distinguish between swimming birds that were associated with vessels and thus active foragers and those swimmers that were not associated with vessels and thus presumably resting. Very few Kittiwakes (less than 5%, German Seabirds at Sea ship database, version 5.07) and only one Guillemot were recorded in association with vessels. Thus, we ignored this parameter for the latter two species.

It should be noted that the length of potential foraging time per day for individual birds exhibits a strong seasonal variation due to the changing number of daylight hours and the varying colony attendance of breeding birds. However, we assumed that individual lengths of time available for foraging at sea were relatively constant across seasons for breeding birds, as number of daylight hours and proportion of time of day spent at the colony are positively correlated such that both effects are offset. For example, the number of daylight hours in summer is roughly double the equivalent number in winter, but on the other hand breeders spend approximately 50% of the daylight hours during summer at the colony (Tasker and Furness 1996), so approximately the same number of hours are spent at sea in daylight during summer and winter.

Seasonal differences in the ratio of flying and swimming birds and in the proportion of vessel association were tested independent of interannual variability by applying a generalized linear mixed model (GLMM; Faraway 2006) written in R (version 2.8.1; http://www.r-project.org/) using the library lme4 (Bates and Sarkar 2007). The model was set as follows: response variable = activity[/vessel association]; predictor = breeding/non-breeding period (& vessel association & interaction between both variables); random effect = year, family = binomial. To obtain an estimate for the model's accuracy, we calculated the root mean square error (RMSE). For all of the species studied, we tested whether higher proportions of flying individuals were recorded during breeding season compared to the rest of the year. Furthermore, we tested the influence of breeding season/non-breeding season on vessel association for Lesser Black-backed Gulls. For this species, we always omitted the winter data from the analysis because the number of individuals observed during this season was negligible but potentially could have biased the results. For auks, we also tested differences in flight activity between autumn and the rest of the year to detect the effect of the moulting and chick-guarding period. Bonferroni correction was applied to account for multiple testing.

Results

Seasonal differences in at-sea activity were evident for all studied species. Analyses revealed significantly higher proportions of flying individuals in summer compared to the rest of the year for all three species.

According to the GLMM, razormots showed significant differences in activity between seasons (Fig. 1, Table 3). The proportion of flying birds was significantly higher during the breeding season and was significantly lower during autumn, with only two flying individuals out of a total of 397 (0.5%). Kittiwake activity varied significantly with season and was highest during summer (Fig. 1, Table 3). Lesser Black-backed Gull activity differed significantly with season and vessel attendance. The proportion of flying individuals was highest during summer and decreased with increasing vessel association (Fig. 1, Table 3). Significant seasonal differences were also recorded for the proportion of Lesser Black-backed Gull vessel association, with the highest values recorded in summer.

Discussion

Methodological aspects

It should be noted that results for proportions of flying and swimming behaviour cannot be fully equated to absolute activity budgets. Considering flying and swimming behaviour only, it is not possible to differentiate between specific foraging behaviours like plunge diving, surface dipping, etc., over the entire data set. Furthermore, no information can be collected on frequency and length of dive bouts of razormots from a moving observation platform. We analysed at-sea surveys only and were thus unable to incorporate information on the length of time spent on land/in the colony and activity at this site. Guillemots and Kittiwakes are truly pelagic seabirds as they do not return to land at night outside the breeding season (Furness and Monaghan 1987). Lesser Black-backed Gulls are not exclusively pelagic in terms of their foraging and resting behaviour. Individuals of this species usually rest on land throughout the whole year, and we assumed that the time spent on land does not differ between the breeding season and the rest of the year.

Lesser Black-backed Gulls often follow vessels in high numbers. This flocking behaviour complicates quantitative analyses, as birds do not behave independently in aggregations. However, as a thorough identification of distinct aggregations at sea is not feasible, this aspect was not included in the analyses.

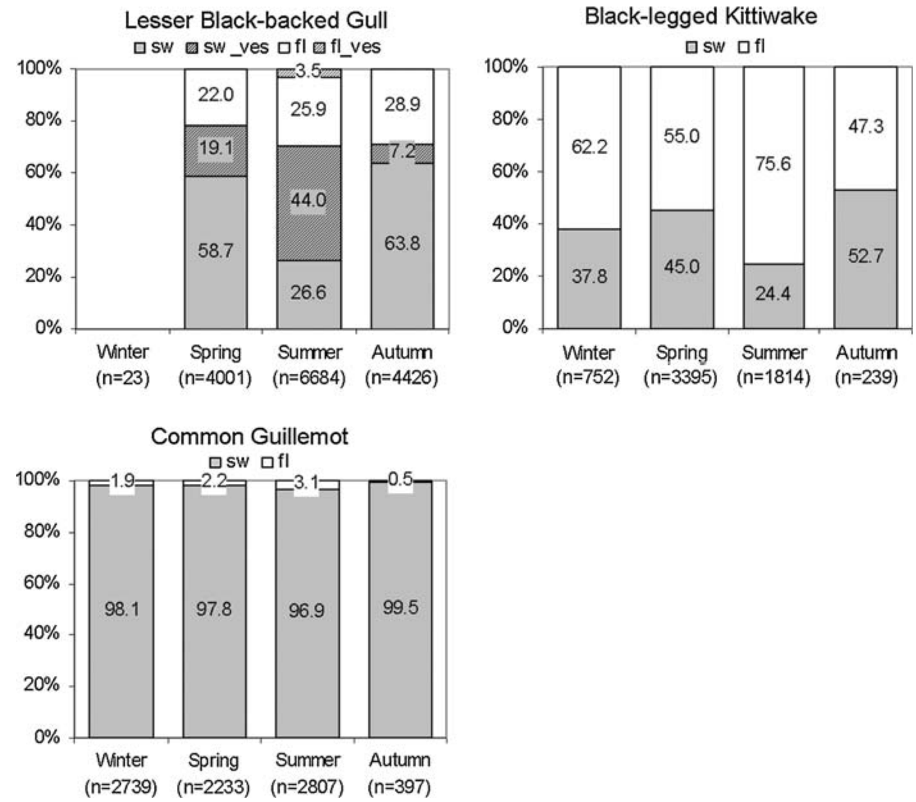

Fig. 1 Season-specific activities of Lesser Black-backed Gull, Black-legged Kittiwake and "razormot" (Common Guillemot/Razorbill) in the German Bight, as recorded during aerial surveys from 2002 to 2006. *sw*, Swimming; *sw_ves*, swimming and associated with fishing vessel; *fl*, flying; *fl_ves*, flying and associated with fishing vessel. Lesser Black-backed Gull activity during winter is not given due to a low sample size

Table 3 Seasonal variation in seabird activity

Species	Response variable	Predictor variables	*p*	Effect size	*z* value	RMSE	*n* birds
Lesser Black-backed Gull	Activity	Summer/rest of year+	***	0.538	10.765	0.41	15111
		Vessel association+	***	−4.249	−11.135		
		Interaction (summer/rest of year and vessel association)	***	1.692	4.345		
Lesser Black-backed Gull	Vessel association	Summer/rest of year	***	1.326	25.979	0.47	15111
Kittiwake	Activity	Summer/rest of year	***	0.837	11.306	0.48	6061
Razormot	Activity	Summer/rest of year	**	0.494	3.017	0.15	8176
Razormot	Activity	Autumn/rest of year	*	−1.827	−2.554	0.15	8176

GLMM results (for details, see "Materials and methods"). The variable "year" was included as a random effect ($n = 5$ years). "Razormot" = Common Guillemot/Razorbill

***Significant at the 0.001 level, **Significant at the 0.01 level, *Significant at the 0.05 level (values are Bonferroni adjusted)

The time of day that the survey is carried out will influence results on distribution (Markones et al. 2008) and activity due to the fact that most seabirds exhibit diurnal patterns of activity (Shealer 2002). This problem will be highlighted in the following for the example of the Kittiwake, but it is assumed to be valid for other species in a similar manner. Breeding Kittiwakes in Scotland showed distinct diurnal differences in activity according to logger data, with the greatest flight activity observed in the morning between 8 and 13 UTC and during late evening (Daunt et al. 2002). Thus, aerial surveys of the present study only covered the periods of greatest activity during the summer (see Table 1). Consequently, estimated activity budgets are likely to overestimate the actual values for the whole day. However, general patterns and differences between seasons should not be influenced by this aspect, as the main time of day sampled was very similar between seasons (Table 1).

As surveys are carried out visually and are thus restricted to daylight conditions, no information could be incorporated on nocturnal activity. Guillemots are thought to be active only during the daytime (Glutz von Blotzheim and Bauer 1999). Studies in the North Sea revealed that Kittiwakes are less active at night both during and outside the breeding season (Garthe and Hüppop 1993, 1996; Daunt et al. 2002), while Lesser Black-backed Gulls frequently forage at fishing vessels during the night both during and outside the breeding season (Garthe and Hüppop 1993, 1996; Mendel et al., in prep.). Studies revealed no information on seasonal differences in diurnal activity.

The relatively high RMSE values of the models for Lesser Black-backed Gulls and Kittiwakes (Table 3) indicate that factors other than season and vessel association have a strong influence on seabird activity. Low RMSE values of models for razormots can however be explained by their rather uniform activity patterns comprising high values of swimming behaviour during all seasons.

Seasonal differences in activity

Our results confirmed hypothesis (1) since we found higher proportions of flying or actively foraging birds in summer compared to the rest of the year for all three species of the different ecological groups. Kittiwakes showed their second-highest activity levels during winter (after breeding season activity levels; see Fig. 1), probably due to the higher thermoregulatory costs of winter and the presumably lower food availability during that season.

Our results support the assumption that breeding birds presumably expend more energy by being engaged in high-cost behaviour like flying and foraging at vessels. It is known that chick-rearing birds increase their working level by 33–50% compared to the non-reproductive period (Drent and Daan 1980). Correspondingly, the proportion of Kittiwakes recorded in flight in the aerial surveys of our study was nearly 20% higher in summer compared to that in spring and more than 25% higher than that in autumn. A quarter of all of the Kittiwakes observed in summer during aerial surveys in our study were swimming. This value is in good agreement with the proportion of the foraging trip spent on the sea surface as recorded by activity loggers for breeding Scottish Kittiwakes (25.0% during the daytime, Daunt et al. 2002) and Kittiwakes in Alaska (21.4 ± 15.8%, Jodice et al. 2003).

In correspondence to hypothesis (2), razormot activity was only slightly (but still significantly) elevated in summer. This may be explained by the fact that alcids mainly forage while swimming and that the proportion of individuals observed flying is generally low in these species. Tremblay et al. (2003) found that breeding Guillemots were resting for only 17% of the time they spent on the surface, and thus were active most of the time (i.e. preening, swimming actively, and interacting with congeners). Flight activity was slightly elevated during the breeding season, probably due to movements between the foraging area and colony, but the difference was very low, as would be expected from a mean foraging radius of only 5–10 km around the single breeding colony in the German Bight on Helgoland (Dierschke et al. 2004). Overall, differences between seasons were very low for this species, and thus probably not of real biological relevance.

The low numbers of flying razormots recorded in autumn correspond to the moulting and chick-guarding period of Guillemots. In correspondence, only 13 individuals out of 1,929 (0.7%) were recorded flying during ship-based surveys in autumn (1990–2006; German Seabirds at Sea database ship v5.07). It is striking that virtually no flying individuals were recorded within a period of 76 days (16 July–30 September), even though adults are flightless for a period of only 45–50 days (Glutz von Blotzheim and Bauer 1999). However, Guillemot chicks, which exhibit intermediate post-hatching development, still need approximately 70 days after leaving the colony to fledge completely (Glutz von Blotzheim and Bauer 1999).

To the best of our knowledge, our study is the first to provide information on seabird activity in a given study area throughout the year using data on a substantial subset of the whole regional population. The method applied here was best suited to assessing activity budgets of surface-feeding species, but was also suited to detecting significant differences in activity between seasons in diving species. We recorded high foraging activity in the breeding season due to high demands, i.e. reproductive costs (self-provisioning plus chick rearing), and elevated foraging activity in winter which was presumably due to reduced food supply and high thermoregulatory costs.

Results on Kittiwake activity correspond well to the activity budgets reported in data logger studies. Thus, our analyses of at-sea activity apparently give reasonable estimates of time–activity budgets.

The extensive dataset used here allows basic theories to be tested and contributes to estimates of energy expenditure at the season level. It fills a gap in existing studies of seabird biology, as information on activity and energy expenditure is mostly collected in the colony and thus only covers the time period when birds are present in the colony. Data logger studies can give information on both periods—time at the colony and time at sea—simultaneously. However, sample numbers are mostly small in these studies and generally cover only a short period within a specific breeding season, while our study gives an overview of the at-sea activity of an entire region during the whole breeding season, and even during the other seasons of the year. However, further progress in microtechnology has recently enabled devices to be attached to seabirds the whole year round, thus producing tracking data over vast ocean areas (e.g. Croxall et al. 2005) and detailed activity data (Catry et al. 2004; Shaffer et al. 2006). Nevertheless, it is worth noting that the birds in such studies carry extra weight, and so they may not always produce unbiased results (e.g. Ropert-Coudert and Wilson 2004).

While results on activity in summer lack information on time spent at the colony and thus can not be equated to actual activity budgets, results on activity budgets outside the breeding season can be directly incorporated into models of energy expenditure and food consumption. However, it is recommended that results on Lesser Black-backed Gulls should be complemented with logger studies in order to obtain data on the time spent on land. The data obtained using this methodology may prove important to improving our understanding of the energetic demands of birds year round, and may also indicate which periods of the year act as bottlenecks. Comparisons of activity patterns between different areas may also enable us to better identify the importance of certain sea areas.

Zusammenfassung

Saisonale Unterschiede in der Aktivität auf See von Seevögeln unterstreichen hohe energetische Kosten zur Brutzeit

Wir untersuchten die saisonalen Unterschiede in der Aktivität auf See beobachteter Heringsmöwen *Larus fuscus*, Dreizehenmöwen *Rissa tridactyla* und Trottellummen *Uria aalge* in der südöstlichen Nordsee (Deutsche Bucht). Die drei Arten repräsentieren dabei verschiedene ökologische Gruppen: die Heringsmöwe die der omnivoren Generalisten, die Dreizehenmöwe die der meeresoberflächennah fressenden Pelagen und die Trottellumme die der pelagischen Seevögel, die ihre Nahrung durch Verfolgungstauchen erbeuten.

Dazu analysierten wir Daten, die bei Seevogelerfassungen vom Flugzeug aus erhoben wurden. Wir unterschieden aktives (fliegend oder nahrungssuchend an Fischkuttern) und inaktives Verhalten (schwimmend). Wir berechneten Aktivitätsbudgets aller drei Arten für jede Jahreszeit und testeten Unterschiede in der Aktivität zwischen den verschiedenen Jahreszeiten. Bei allen Arten wurden signifikante Unterschiede in der Aktivität zwischen den verschiedenen Jahreszeiten festgestellt. Die höchsten Aktivitätsraten traten während der Brutsaison auf. Außergewöhnlich niedrige Zahlen fliegender Alken wurden im Herbst festgestellt, die auf die Mauser und das Führen noch flugunfähiger Küken zurückzuführen sind. Unsere Ergebnisse unterstreichen die hohen Energieanforderungen der Brutsaison, die in einer erhöhten Nahrungssuch- und Flugaktivität resultieren.

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