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Migrating shorebird killed by raptor at 3000 m above ground as revealed by high-resolution tracking

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Recent tracking technology has revealed that some birds fly at extreme altitudes up to and above 7000 m above sea level (asl) during nonstop migration flights (Lindström et al., 2021; Sjöberg et al., 2021). An untested hypothesis put forward is that birds migrate this high above the ground to avoid encountering predators. However, information about predation danger during the migratory flight is scant, and the altitudes where migrants are at risk are unknown.

While migration enables animals to exploit favorable habitat conditions in various locations throughout the year to optimize overall fitness (Lack, 1968), it can also be costly and is often associated with higher mortality rates (Klaassen et al., 2014). A significant factor contributing to these high mortality rates is the increased risk of predation during migration (Lindström, 1989; Sillett & Holmes, 2002; Walter, 1979). Consequently, safety is considered an important evolutionary driver of avian migration strategies (Alerstam et al., 2003; Alerstam & Lindström, 1990; Lank et al., 2003; Ydenberg et al., 2004).

In birds, predation has mostly been studied at migratory stopover sites (Dierschke, 2003; Lindström, 1989), but information about predation risk during the migratory flight is largely lacking, especially concerning at what altitudes migrants are at risk. It was recently revealed that during long nonstop flights, some migrants

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ascend at dawn to diurnal flight altitudes up to and above 7000 m asl (Lindström et al., 2021; Sjöberg et al., 2021). These studies propose that the birds try to avoid being predated by flying very high above the ground. Eleonora's Falcons *Falco eleonorae,* which specialize in hunting migratory passerines, have been recorded to make flights up to 3500 m (Xirouchakis & Panuccio, 2019), but the knowledge on how high avian predators ascend to hunt is very limited.

Using GPS trackers with on-board accelerometry, we tracked Arctic-breeding Grey Plovers *Pluvialis squatarola* (Figure 1a,b) migrating across Northern Europe. In January 2023, we tagged eight adult Grey Plovers with Druid MINI 2G transmitters on the island of Griend (53°15′ N, 5°15′ E) in the Dutch Wadden Sea. Tags were attached using leg-loop harnesses constructed from flattened spectra ribbon (2.5 mm width) and aluminum crimps (combined mass of transmitter and harness <8 g, equaling <5% of body mass). The solar-powered transmitters record GPS positions (including altitude), and ODBA (overall dynamic body acceleration, a measure for activity (Wilson et al., 2006), hereafter "body acceleration" for short). Data were transferred via the 2G GSM network. Interval settings varied from 2 to 24 h for GPS positions and 1–30 min for body acceleration measurements. The onboard tri-axial accelerometer sampled data continuously at 25 Hz which were summarized into one body acceleration value every 10 s following Wilson et al. (2006). These values were then used to calculate average body acceleration values based on the set interval (e.g., mean of 6 values for 1-min body acceleration setting).

FIGURE 1 (a, b) 11:21 25-01-2023, Griend, The Netherlands. The Grey Plover photographed upon release on the island of Griend in the Dutch Wadden Sea in January 2023, equipped with color bands (a) and a Druid MINI 2G transmitter (b). (c) 12:17 04-06-2023, Lund municipality, Sweden. The transmitter and several of the colors bands found next to the remains of the Grey Plover near the Peregrine Falcon nest in Southern Sweden in June 2023. Photographs: Thomas K. Lameris (a, b), Arne Hegemann (c).

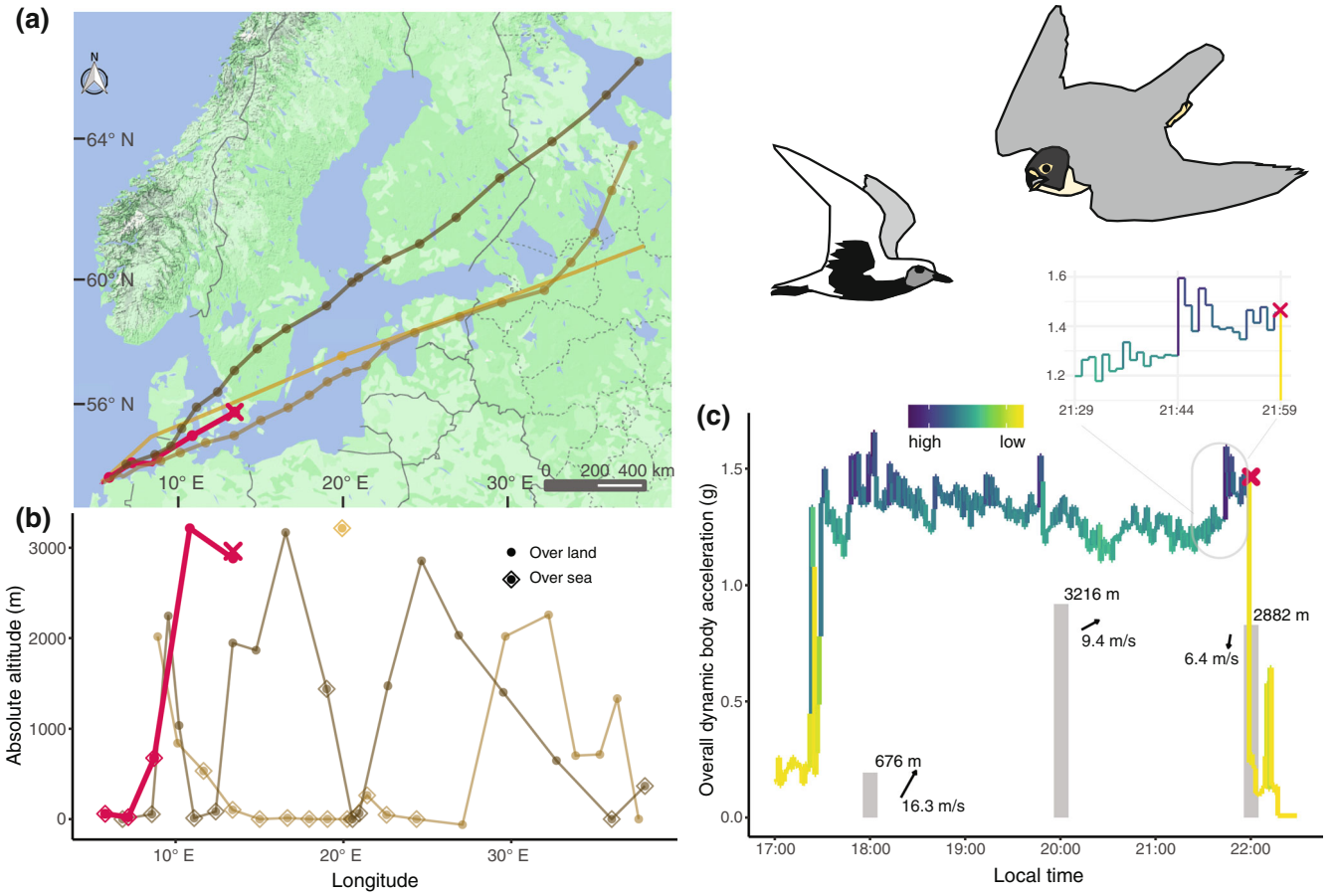

FIGURE 2 Spring migration routes (a) and flight altitude (b) of four Grey Plovers tracked across Northern Europe by GPS-GSM transmitters with 2-h sampling interval (except one individual with 24-h interval). The track of the predated plover is highlighted in red, and the predation location is marked by a cross. Positions above land are marked with dots, positions above sea are marked with diamonds. (c) Overall dynamic body acceleration of the predated individual during the 5 h prior to predation, including an inset of the last 30 min. Information from three GPS fixes of the predated individual is annotated in the bottom of the graph, including flight altitude (gray bars), flight course (direction of arrows), and flight speed (in meters per second). Illustrations: Thomas K. Lameris.

At 21:58 local summer time on May 27 (25 min after sunset), one of the tagged birds suddenly stopped its migratory flight (Figure 2a,b). At the same moment, the body acceleration signal (1-min average) of the tracking device on this plover made a steep drop from 1.45 to 0.27 g (Figure 2c). Two minutes later (i.e., 22:00), the logger recorded a GPS fix at an altitude of 2882 m above ground (about 2900 m asl). Additional information from this fix was in strong contrast with the previous fixes: a change in course from 64° (NE) to 194° (SW) and a decrease in speed of flight from 14.4 ± 4.1 m/s to 6.4 m/s (Figure 2c). The subsequent GPS fix at 00:00 h on May 28 and all subsequent fixes came from a single position 8 km away.

Here, the tag and remains of the bird (Figure 1c) were found within 200 m of a peregrine nest, undoubtingly suggesting predation by a peregrine falcon (*Falco peregrinus*) as the cause of death. Together this suggests that the plover was captured by the falcon at 21:58. Considering the 2-min delay of GPS fix after the predation, the predation altitude was at least 2882 m above ground level (Figure 2c) but could have been higher. In the 15 min right before the predation event (21:43–21:58), the plover displayed increased body acceleration (1.44 ± 0.07 g, Figure 1c), which was significantly higher than the previous 15-min period body acceleration (1.26 ± 0.04 g, $t(22) = -8.6$, $p < 0.0001$). Increased body acceleration is associated with increased flight intensity (Krishnan et al., 2022), which could indicate that the plover spotted the predator peregrine falcon at around 21:43 and made an attempt to escape.

Peregrines use various hunting techniques to capture birds in flight (Zoratto et al., 2010), including a characteristic surprise stoop dive from above, which requires the peregrine to ascent to higher altitudes than its prey to hunt. In the case of the observed predation event, the potential attempt to escape (based on the observed 15-min increase in dynamic body acceleration) of the Grey Plover suggests that the peregrine would have used

a pursuit tactic, which is also commonly observed (Dekker, 2009; Zoratto et al., 2010).

We also compared migration timing and flight altitude of the predated individual with three other tracked individuals from which we received data for the period from departure from the Wadden Sea and up to passage into the Russian Arctic (37° E). The route taken by the predated plover was similar to that of the other tracked individual plovers (Figure 2a). The predated plover started its migratory flight on May 26, which was also comparable with the other three tracked individuals (May 26–28). All four plovers flew higher above land (mean flight altitude 1726 ± 966 m, Figure 2b) than above sea (302 ± 717 m, Figure 2b). The altitude at which the predated plover was captured (2882 m) was at the higher end of the altitudinal range of flight over land (0–3216 m) in our dataset.

Although in-flight predation of birds in active migration is indirectly documented through the large numbers of migratory prey species in the diet of falcons (Xirouchakis et al., 2019; Zuberogoitia et al., 2013), direct evidence is limited to ground-based observations, by necessity limiting the altitudes at which predation events can be recorded (Rudebeck, 1950, 1951). This limitation is lifted by the recent application of ever lighter high-resolution tracking devices on small-bodied birds, enabling us to remotely record in-flight predation (e.g., Bom et al., 2023). The observed predation event constitutes an exceptional record of high-altitude hunting by Peregrine Falcons. These falcons are specialized in hunting birds and capturing them in flight (Xirouchakis et al., 2019; Zuberogoitia et al., 2013). During migratory flight, Peregrine Falcons can reach altitudes up to 5600 m (Dixon et al., 2017), but up to which altitude they hunt is unclear. GPS-tracking of Greater Noctule Bats *Nyctalus lasiopterus*, known to prey on migratory birds (Ibáñez et al., 2001), has unveiled they forage up to 1659 m above ground level (Nadő et al., 2019). In areas and periods with sufficient prey availability at high altitude (e.g., migration corridors during shorebird migration), hunting at high altitudes may be a profitable strategy.

While predation risk is considered an important evolutionary driver of migration strategies (Alerstam & Lindström, 1990; Lank et al., 2003; Ydenberg et al., 2004), its role in shaping flight altitudes remains only speculative. The application of high-resolution tracking now makes it possible to address questions on where, when, and up to which altitude birds risk predation during migratory flight, and for example whether flying at extreme altitudes during the day may be a successful adaptive strategy to avoid predators. Our observation suggests that this may not always be the case, as increasing flight altitude up to 3000 m above ground is clearly not enough for migrants to avoid predation risk.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data cannot be made publicly available due to the protected status of nesting Peregrine falcons in Sweden. Tracking data are owned by the Netherlands Institute of Ecology (NIOO-KNAW) and archived on Movebank under the study name "Grey Plover_ArcticMigrants_Wadden Sea" (Movebank ID: 2624192779) and can be requested by contacting the Principal Investigator via the contact option on the Movebank study page: https://www.movebank.org/cms/webapp?gwt_fragment=page=studies,path=study2624192779.

ETHICS STATEMENT

Permits to catch, handle, and tag Grey Plovers were granted to the NIOZ under protocol number AVD80200202215943.

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REFERENCES

Alerstam, T., A. Hedenström, and S. Åkesson. 2003. "Long-Distance Migration: Evolution and Determinants." *Oikos* 103(2): 247–260. https://doi.org/10.1034/j.1600-0706.2003.12559.x.

Alerstam, T., and Å. Lindström. 1990. "Optimal Bird Migration: The Relative Importance of Time, Energy, and Safety." In *Bird Migration*, edited by E. Gwinner Dixon, H. H. T. Prins, and T. Namgail, 331–351. Berlin, Heidelberg: Springer.

Bom, R. A., Å. Lindström, and T. Piersma. 2023. "Predation Danger during Active Migration: Insights from a Tagged Bar-Tailed Godwit Depredated by a Breeding Peregrine Falcon." *Wader Study* 130(1): 78–81. https://doi.org/10.18194/ws.00294.

Dekker, D. 2009. "Hunting Tactics of Peregrines and Other Falcons." PhD thesis, Wageningen University.

Dierschke, V. 2003. "Predation Hazard during Migratory Stopover: Are Light or Heavy Birds under Risk?" *Journal of Avian Biology* 34(1): 24–29. https://doi.org/10.1034/j.1600-048X.2003.03049.x.

Dixon, A., L. Rahman, A. Sokolov, and V. Sokolov. 2017. "Peregrine Falcons Crossing the Roof of the World." In *Bird Migration across the Himalayas: Wetland Functioning amidst Mountains and Glaciers* 53–67. Cambridge: Cambridge University Press.

Ibáñez, C., J. Juste, J. L. García-Mudarra, and P. T. Agirre-Mendi. 2001. "Bat Predation on Nocturnally Migrating Birds." *Proceedings of the National Academy of Sciences of the United States of America* 98(17): 9700–9702.

Klaassen, R. H. G., M. Hake, R. Strandberg, B. J. Koks, C. Trierweiler, K. M. Exo, F. Bairlein, and T. Alerstam. 2014. "When and Where Does Mortality Occur in Migratory Birds? Direct Evidence from Long-Term Satellite Tracking of Raptors." *Journal of Animal Ecology* 83(1): 176–184. https://doi.org/10.1111/1365-2656.12135.

Krishnan, K., B. Garde, A. Bennison, N. C. Cole, E.-L. Cole, J. Darby, K. H. Elliott, A. Fell, A. Gómez-Laich, and S. De Grissac. 2022. "The Role of Wingbeat Frequency and Amplitude in Flight Power." *Journal of the Royal Society Interface* 19(193): 20220168. https://doi.org/10.1098/rsif.2022.0168.

Lack, D. L. 1968. "Bird Migration and Natural Selection." *Oikos* 19(1): 1–9.

Lank, D. B., R. W. Butler, J. Ireland, and R. C. Ydenberg. 2003. "Effects of Predation Danger on Migration Strategies of Sandpipers." *Oikos* 103(2): 303–319. https://doi.org/10.1034/j.1600-0706.2003.12314.x.

Lindström, Å. 1989. "Finch Flock Size and Risk of Hawk Predation at a Migratory Stopover Site." *The Auk* 2(April): 225–232.

Lindström, Å., T. Alerstam, A. Andersson, J. Bäckman, P. Bahlenberg, R. Bom, R. Ekblom, et al. 2021. "Extreme Altitude Changes between Night and Day during Marathon Flights of Great Snipes." *Current Biology* 31(15): 3433–39.e3. https://doi.org/10.1016/j.cub.2021.05.047.

Naďo, L., D. Lőbbová, E. Hapl, M. Celuch, M. Uhrin, M. Šara, and P. Kaňuch. 2019. "Highly Selective Roosting of the Giant Noctule Bat and its Astonishing Foraging Activity by GPS Tracking in a Mountain Environment." *Mammal Research* 64: 587–594.

Rudebeck, G. 1950. "The Choice of Prey and Modes of Hunting of Predatory Birds with Special Reference to Their Selective Effect." *Oikos* 2(Fasc. 1): 65–88.

Rudebeck, G. 1951. "The Choice of Prey and Modes of Hunting of Predatory Birds with Special Reference to their Selective Effect." *Oikos* 3(Fasc. 2): 200–231.

Sillett, T. S., and R. T. Holmes. 2002. "Variation in Survivorship of a Migratory Songbird throughout its Annual Cycle." *Journal of Animal Ecology* 71(2): 296–308. https://doi.org/10.1046/j.1365-2656.2002.00599.x.

Sjöberg, S., G. Malmiga, A. Nord, A. Andersson, J. Bäckman, M. Tarka, M. Willemoes, et al. 2021. "Extreme Altitudes during Diurnal Flights in a Nocturnal Songbird Migrant." *Science* 372(6542): 646–48. https://doi.org/10.1126/science.abe7291.

Walter, H. 1979. *Eleonora's Falcon: Adaptations to Prey and Habitat in a Social Raptor*. Chicago and London: University of Chicago Press.

Wilson, R. P., C. R. White, F. Quintana, L. G. Halsey, N. Liebsch, G. R. Martin, and P. J. Butler. 2006. "Moving towards Acceleration for Estimates of Activity-Specific Metabolic Rate in Free-Living Animals: The Case of the Cormorant." *Journal of Animal Ecology* 75(5): 1081–90. https://doi.org/10.1111/j.1365-2656.2006.01127.x.

Xirouchakis, S. M., H. Alivizatos, E. Georgopoulou, A. Dimalexis, P. Latsoudis, D. Portolou, G. Karris, et al. 2019. "The Diet of the Eleonora's Falcon (*Falco eleonorae*) in the Aegean Archipelago (Greece)." *Journal of Natural History* 53(29–30): 1767–85. https://doi.org/10.1080/00222933.2019.1668978.

Xirouchakis, S. M., and M. Panuccio. 2019. "Hunting Altitude of Eleonora's Falcon (*Falco eleonorae*) over a Breeding Colony." *Journal of Raptor Research* 53(1): 56–65.

Ydenberg, R. C., R. W. Butler, D. B. Lank, B. D. Smith, and J. Ireland. 2004. "Western Sandpipers Have Altered Migration Tactics as Peregrine Falcon Populations Have Recovered." *Proceedings of the Royal Society of London. Series B: Biological Sciences* 271(1545): 1263–69. https://doi.org/10.1098/rspb.2004.2713.

Zoratto, F., C. Carere, F. Chiarotti, D. Santucci, and E. Alleva. 2010. "Aerial Hunting Behaviour and Predation Success by Peregrine Falcons Falco Peregrinus on Starling Flocks Sturnus Vulgaris." *Journal of Avian Biology* 41(4): 427–433. https://doi.org/10.1111/j.1600-048X.2010.04974.x.

Zuberogoitia, I., J. E. Martínez, J. A. González-Oreja, J. F. Calvo, and J. Zabala. 2013. "The Relationship between Brood Size and Prey Selection in a Peregrine Falcon Population Located in a Strategic Region on the Western European Flyway." *Journal of Ornithology* 154(1): 73–82. https://doi.org/10.1007/s10336-012-0872-9.

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