



Volume-concentrated searching by an aerial insectivore, the common swift, *Apus apus*

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How predators search for prey is a cornerstone question in behavioural ecology, which has yet to be investigated for animals foraging in 3D airspace. Do insectivorous birds such as swifts (Apodidae), swallows and martins (Hirundinidae) use similar strategies to those performed by terrestrial predators in 2D, or do they rely on different spatial search strategies because of some properties of the aerial open space? We addressed this question in the common swift, one of the most aerial birds, using a novel 3D optical tracking method. The analysis of fine-scale flight tracks revealed how birds distribute their presence in 3D space while foraging near their breeding colony. Common swifts concentrated the time spent per volume unit by adopting a tortuous path, and, to a much lesser extent, by decreasing their movement speed. By independently observing the birds' posture on tracking images, we were able to identify the occurrence of putative prey captures along flight tracks. We show that swifts' presence was concentrated mainly in the vicinity of prey captures, unveiling a volume-concentrated search (VCS) strategy in this aerial insectivore. This is an extension in 3D of the area-concentrated search classically described in terrestrial 2D space. VCS can (but does not necessarily) take place in thermal updrafts, where small insects can be concentrated in patches. In contrast to terrestrial and aquatic predators that can easily slow down or stop their movement in profitable places, a different speed–cost relationship underlying aerial movement prevents swifts from stopping in prey patches and explains why these birds rely mainly on movement tortuosity to perform intensive search. Our study thus shows how some physical properties of the environment can modulate the way an animal concentrates its search in profitable places.

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Since the airspace has been recognized as a habitat for flying animals (Diehl, 2013), aero-ecology receives growing interest, supported by the advent of radar techniques for scanning the aerosphere for birds, bats and insects (e.g. Frick et al., 2012; Chapman et al., 2015; Horton, Doren, Stepanian, Farnsworth, & Kelly, 2016; Wainwright, Stepanian, Reynolds, & Reynolds, 2017) and animal-borne miniaturized loggers for tracking individual birds and bats along their local or migratory movements (e.g. Mora, Ross, Gorsevski, Chowdhury, & Bingman, 2012; Amélineau et al., 2014; Åkesson, Bianco, & Hedenström, 2016; Weller et al., 2016). An important subject in aero-ecology is aerial predation of insects by small specialized birds such as swifts (Apodidae), swallows and martins (Hirundinidae), which has a strong impact on insect

population regulation (Kelly, Bridge, Frick, & Chilson, 2013; Helms, Godfrey, Ames, & Bridge, 2016a). However, studies of foraging movements in aerial insectivores are still scarce, because of the technical difficulties in tracking small birds with both fine spatio-temporal resolution and sustained duration. Warrick, Hedrick, Biewener, Crandell, and Tobalske (2016) used sophisticated optical tracking to study low-altitude three-dimensional (3D) foraging manoeuvres in barn swallows, *Hirundo rustica*, at very high resolution (100 Hz) but for short durations (<5 s), whereas, using miniature loggers and postflight diet analysis, Helms et al. (2016a, b) measured foraging in the purple martin, *Progne subis*, for whole flights, but restricted to a single dimension (altitude). Still, studying 3D movements of these small birds while they search for, find and catch prey would be valuable for understanding aerial insectivores' foraging behaviour, that is, how they explore and exploit food resources in airspace.

In numerous species, animals tend to shift from extensive to intensive searching after the detection of a prey item. Extensive

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searching corresponds to transit, whereas intensive searching leads to a concentration of the searching in the vicinity of the item previously detected. It is often referred to, in 2D space, as area-concentrated (or area-restricted) searching (ACS; e.g. Benhamou, 1992, 1994), and therefore in 3D space can be referred to as volume-concentrated searching (VCS). This shift corresponds to a behavioural adaptation to the heterogeneity of the environment: prey items being often aggregated in patches, the probability of detecting a new prey item close to the previous one is higher than at a random location in the environment. It classically involves increasing the path tortuosity, which allows the predator to remain in close spatial proximity to the location of the previously detected item, and decreasing the speed, which allows it to better detect new, more-or-less cryptic items (Knoppien & Reddingius, 1985). However, a lower speed also results in a lower encounter rate, so that the detection rate, and therefore the foraging efficiency, is not necessarily improved (Benhamou, 1992). Reduced speed usually observed in intensive searching may be more the consequence of the extra time required to handle prey than a means to improve foraging efficiency. In this classical view, where prey are immobile (or move slowly with respect to the predator), shifting from extensive to intensive searching after detecting a prey item is certainly an efficient strategy (Benhamou, 1992, 1994), even when prey are hard to detect (Benhamou & Collet, 2015). However, when prey can move faster to escape predators, it may be preferable to avoid performing ACS. For example, after capturing an item, waders looking for immobile prey perform ACS, whereas others looking for prey able to suddenly hide when disturbed move quickly off the area (Dias, Granadeiro, & Palmeirim, 2009). Only a few studies have focused on shifts from extensive to intensive searching in 3D space, especially in marine mammals (e.g. Le Bras, Jouma'a, Picard, & Guinet, 2016, 2017), and, to our best knowledge, none in aerial species. Yet, the constraints are very different, as the mechanical power required to perform slow flight is very high (Tobalske, 2007), and many flying species are unable to perform sustained hovering flight (i.e. stop movement). For example, in common swifts, wind tunnel experiments show that there is a minimal steady flight speed, in both flapping and gliding flight (Henningson et al., 2011; Henningson & Hedenström, 2011). In this context, intensive searching can be expected to rest mainly on higher path tortuosity, with limited change in speed. One should also consider that such aerial predators that hunt in open spaces probably do not need to slow down to detect prey, which should be detectable from a large distance. Thus, in contrast to what occurs with predators looking for hidden prey that can be detected only from a much shorter distance than the patch radius, the perception of the whole patch should facilitate its exploitation. On the other hand, intercepting each prey in flight can require high manoeuvrability, which in animal locomotion is often inversely related to speed (Warrick, 1998; Hedenström & Rosén, 2001; Moore & Biewener, 2015; Clemente & Wilson, 2016). In the present study, we aimed to assess how local flight movements in common swifts reflect their search behaviour. Do common swifts use a VCS foraging strategy in 3D space? If they do so, is aerial VCS based on path tortuosity increase, speed decrease, or both?

Common swifts' level of adaptation to the aerial medium is uncommon. Starting with basic morphology, this species and other Apodidae present a striking allometry with reduced legs (explaining the taxon name) and a very long hand segment (Lack, 1956; Warrick, 1998; Tobalske, 2010). Moreover, their wings can drastically change shape, providing a 'morphing' flight apparatus that combines the performance of several other bird species (Lentink et al., 2007). Their feathers have a rough surface that favours both stiffness and aerodynamism (Lentink & de Kat, 2014; van Bokhorst, de Kat, Elsinga, & Lentink, 2015). Such aerodynamic refinements result in unique aerial

behaviour: common swifts are small birds with immense flying skills, which spend most of the day and night flying, sometimes not landing for 10 months (Hedenström et al., 2016). Egg laying, incubation and feeding young (Lack & Lack, 1951) are the sole activities that keep common swifts terrestrial for some of the time for approximately 2 months a year. Hence, they perform most daily activities in mid-air, including foraging, social bonding (Farina, 1988; Henningson et al., 2010) and probably sleeping, during overnight 'roosting' where the birds settle their flight into the head wind (Bäckman & Alerstam, 2001, 2002; Rattenborg, 2017). Twice daily, common swifts also perform enigmatic high-altitude twilight ascents (Hedenström et al., 2016), possibly to profile atmospheric conditions or to increase their visual range of the ground (Dokter et al., 2013). During migration, common swifts can travel at speeds up to 650 km/day (Åkesson, Klaassen, Holmgren, Fox, & Hedenström, 2012), efficiently orienting their flight according to wind conditions (Karlsson, Henningson, Bäckman, Hedenström, & Alerstam, 2010; Hedenström & Åkesson, 2017). During the breeding season, nest material collection and mating can also be performed airborne (Lack, 1956; Gory, 1994).

The flight of common swifts has been studied at various temporal and spatial scales, depending on the question addressed and the technique used. Instantaneous biomechanical performance has been measured in wind tunnel experiments using decoys (Lentink et al., 2007) or living swifts (Henningson, Spedding, Hedenström, 2008, 2011; Henningson & Hedenström, 2011). In the field, using 3D optical tracking at close range (ca. 8 m), the top speed of common swifts during their fast social flights ('screaming parties') was shown to reach 31 m/s (Henningson et al., 2010). Tracking-radar-based studies have yielded tracks at the scale of several kilometres, with 0.5 Hz location sampling frequency (Bäckman & Alerstam, 2001, 2002; Henningson et al., 2009), which provide information on flight speeds and orientation of birds relative to the wind. Similar information has been derived from tracking swifts every few seconds with an 'Ornithodolite' (i.e. a laser rangefinder coupled with a magnetic compass and an inclination sensor; Hedenström & Åkesson, 2017). Weather radar was also used to measure the altitude of swift flocks every 5 min throughout the breeding season and to characterize their twilight ascents (Dokter et al., 2013). Last, a recent technique using miniature light level loggers (GLS) attached to the animal (Åkesson et al., 2012, 2016), possibly coupled with accelerometers to detect landing (Hedenström et al., 2016), was used to track individual annual migration routes from Europe to Africa and back, with a sampling frequency of two locations per day, and a spatial uncertainty in the order of 100 km. Better accuracy and higher sampling frequency would require GPS loggers, which are, however, currently still too heavy for tracking such a small species (ca. 45 g adult body mass; Åkesson et al., 2012). As a result, and even though all these studies make the common swift one of the most scrutinized flying species, we still know little about the spatial behaviour of swifts during their daily local activities.

Recent developments in 3D optical tracking in the field, using several fixed cameras (Therault et al., 2014; Jackson, Evangelista, Ray, & Hedrick, 2016) or a single camera for rotational stereovideography (RSV; de Margerie, Simonneau, Caudal, Houdelier, & Lumineau, 2015), make it possible to track flying animals in 3D with a high sampling frequency (>1 Hz), at distances of 10–1000 m depending on the tolerable location error. These noninvasive, tag-less optical approaches are promising methods to study flight behaviour, such as tandem flight behaviours in cliff swallows, *Petrochelidon pyrrhonota* (Shelton, Jackson, & Hedrick, 2014) or collective flight behaviour in chimney swifts, *Chaetura pelagica* (Evangelista, Ray, Raja, & Hedrick, 2017). Here we used RSV to track individual common swifts performing aerial foraging flights near

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