Fly-and-forage strategy in the bat *Pipistrellus nathusii* during autumn migration

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Populations of *Pipistrellus nathusii* (Nathusius's bat), an insectivorous aerial-hawking species that breeds in north-eastern Europe, perform long-distance migrations between breeding sites and hibernation areas in central and southern Europe. The feeding strategy of migrating *P. nathusii* was investigated in Latvia on the east coast of the Baltic Sea, exploring evidence for and against two non-mutually exclusive predictions that i) the bats feed shortly after dusk at highest aerial insect activity and continue to migrate thereafter or ii) apply a 'fly-and-forage' strategy and frequently interrupt their migration flight to feed. Echolocation calls and feeding buzzes of *P. nathusii* were recorded throughout the night from August until September on a known migration flyway over coastal dunes and at potential foraging sites in adjacent woodlands, over meadows and wetlands. The results indicate that *P. nathusii* applies a fly-and-forage strategy along the Baltic coast. However, a threshold in aerial insect availability may exist, below which no foraging occurs and migration continues.

Key words: Baltic Sea, feeding strategy, Latvia, Pape Ornithological Research Station

Introduction

In autumn, some bat species from Fennoscandia and north-eastern Europe, such as *Pipistrellus nathusii* (Nathusius's bat)*,* migrate south along the Baltic coast towards central and southern Europe to overwinter (Popa-Lisseanu and Voigt, 2009). Recoveries of wing-banded individuals (Strelkov, 1969; Pētersons, 2004; Hutterer *et al.*, 2005) and stable hydrogen isotope composition analysis (Voigt *et al.*, 2012*a*) suggest that this migration can be as long as 2000 km between summer breeding and winter hibernation areas (maximum distance documented from recapture data is 1905 km — see Pētersons, 2004). Meeting energy demands of migration is presumably of primary importance for survival and reproductive success of the bats. Bats are able to forage and feed during flight, thus replenishing energy loss due to flight by rapid mobilisation and oxidation of ingested nutrients (Welch *et al.*, 2008; Voigt *et al.*, 2010; Suarez *et al.*, 2011). Direct and indirect observations suggest that migrating bats may feed while migrating (Ahlén *et al.*, 2009; Valdez and Cryan, 2009). Prior to hibernation and migration bats feed intensively to store fat (Kunz *et al.*, 1998; McGuire *et al.*, 2009; Šuba *et al.*, 2011). Stored fat is also utilised for energy during migration flights, complementing or substituting the exogenous fuel source obtained directly from consumed prey (Voigt *et al.*, 2012*b*).

By acoustically monitoring migrating *P. nathusii* in the field at the Baltic coast of Latvia, we investigated how bats allocate their time between migration flights and foraging efforts. At high latitudes, nocturnal insect abundances typically peak shortly after dusk and then decline until a second peak occurs just before sunrise (Taylor, 1963). This bimodal pattern is usually reflected in the foraging activity of aerial-hawking bats (Racey and Swift, 1985; Rydell *et al.*, 1996). We may therefore expect that bats on migration would allocate most feeding efforts to the period after dusk and before dawn, and show a reduced feeding rate in between. However, if insect abundance remains high throughout the night, they may apply a 'fly-and-forage strategy' en-route (Strandberg and Alerstam, 2007), perhaps interrupting the migration flight to feed whenever rich food patches are encountered.

MATERIALS AND METHODS

The study was undertaken at Pape Ornithological Research Station at the Baltic coast of Latvia (56°09'57"N, 21°01'02"E), where autumn migration patterns of bats have been documented over the preceding two decades (Pētersons, 2004). The study area consists of low sand dunes covered by unmanaged *Pinus sylvestris* (scots pine) woodlands and grasslands crossed by dirt roads, occasional buildings and Lake Pape with adjacent marshlands. The lake is connected to the sea at its southern part through a canal with natural vegetation such as *Salix* spp. (willows) and *Phragmites australis* (syn. *P. communis*; reeds).

Observations were made between the 5th of August and the 13th of September 2010 within a 4.5 km² area (Fig. 1). The selected study sites represented the principal habitats of the study area: 1) 'the dune site', located on sand dunes ca. 100 m from the coastline, 2) 'the canal site', located at the bank of the canal, 3) 'the marsh site', located in marshland at the western shore of the lake, 4) and 5) 'meadow sites 1 and 2', located on open grasslands, 6) and 7) 'forest sites 1 and 2', located in *P. sylvestris* woodlands. The sites were separated by at least 200 m. At the dune site, surveys of autumn bat migration have been conducted annually during 1993–2012. Previously observed flights of *P. nathusii* at this site are generally fast, straight and nearly always directed towards the south over the dunes along the coast, hence the dune site was identified as a candidate for the bats' migration flyway. *P. nathusii* is by far the most abundant

bat species at this site in August and September (89% of all captured individuals — see Hutterer *et al*., 2005).

Acoustic recordings of echolocation calls were made at each of the seven study sites, using four digital sound recorders VN-550PC (Olympus Imaging America Inc., Pennsylvania, USA) connected to heterodyne ultrasound detectors D-200 (Pettersson Elektronik AB, Uppsala, Sweden). The detectors were assumed to have equal sensitivity and set to 40 kHz, which in most cases is appropriate to recognise sonar calls of *P. nathusii* (clear and 'wet' sounds) and easily distinguish them from those of other species (obscure or 'dry' sounds at this frequency). Connected devices were kept in a plastic 13 × 13 × 6 cm box to protect the equipment from moisture and a 0.5 cm diameter hole was made for the microphone of the detector (Ahlén *et al*., 2007). The microphone was directed with an angel (30–45º) upwards and exposed to the north (at the dune site, meadow sites and the marsh site), randomly (at forest sites) or towards the water (at the canal site). The four boxes were either placed on the ground (Meadow Sites) or on a pole 2 m above the water level (Marsh Site) or in trees 2, 2, 5 and 7 m above the ground (the Dune, Canal and two Forest Sites, respectively). At the Dune Site recordings were made every night, but the other sites were surveyed on alternative nights — Forest Site 1, Meadow Site 1 and Canal Site were surveyed on the same night followed by Forest Site 2, Meadow Site 2 and Marsh Site on the following night. Normally recordings were conducted from sunset until sunrise. Altogether 88 recordings were used in the analysis. Recordings that lasted for less than six hours due to
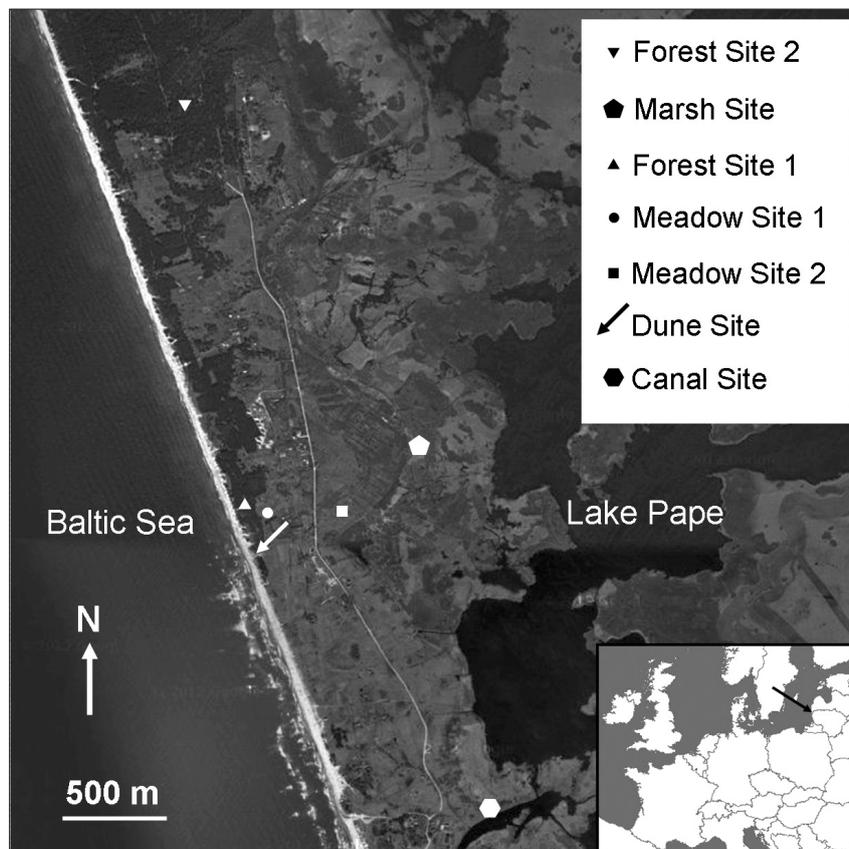

FIG. 1. The study area and location of study sites (the background satellite image obtained from Cnes/Spot Image, DigitalGlobe, GeoEye 2012)

discharge of the batteries or were heavily disturbed by noise such as katydid/bush-crickets chirring, strong wind or heavy rain were omitted ($n = 68$).

The audio recordings were analysed with the sound editing software Sound Forge 9.0 (Sony Creative Software Inc., Middleton, UK). They were divided into five-minute sections (further referred as 'sections'), for which the following were registered: a) duration of continuous echolocation call sequences (further referred as 'sonar sequences'), b) time of occurrence (in minutes after sunset) and c) presence or absence of so called 'feeding buzzes', which unambiguously indicate attempted feeding (Surlykke *et al.*, 2003). Sonar sequences were easily distinguishable by silent intervals between them (> 4 s). No attempts were made to distinguish passes of individual bats, since there were no visual information and two or more bats occasionally passed by simultaneously. Occasional sonar sequences and associated feeding buzzes of species other than *P. nathusii* were not considered in the analysis.

Statistical analyses were carried out using the program R (version 2.13.0; The R Foundation for Statistical Computing, 2011). The cumulative duration of all sonar sequences per hour and the number of sections containing feeding buzzes per hour were used as indices of activity and feeding intensity, respectively. Feeding rate was expressed as number of sections containing feeding buzzes divided by the number of all sections that contained echolocation calls, which also equals to probability that passing bats would interrupt their flight and feed. For the null hypothesis, a constant feeding rate each hour throughout the night was assumed and fit to a uniform distribution was tested using Pearson's chi-squared test. Kruskal-Wallis (K-W) rank sum tests were used to compare different parameter values among the study sites. Pair-wise comparisons were made by Wilcoxon rank sum test with continuity correction. Significance of relationships was tested by Pearson's product moment correlation, for which data normality was tested by Shapiro-Wilk normality test.

RESULTS

In total, 88 recordings (740h) were analysed. Every evening the first sonar calls of *P. nathusii* were recorded 40–100 minutes after sunset (Table 1), with significant differences among the sites (Kruskal-Wallis test, $\chi^2 = 36.5$, *d.f.* = 6, $P < 0.001$). Generally at the two forest sites, the first sonar calls were recorded earlier than at the open sites. During the study period from the 5th of August until the

13th of September, night length (sunset to sunrise) increased from 8.1 to 10.9h, but there was no significant increase in the length of the nocturnal activity period of *P. nathusii* (Pearson's product-moment correlation, $r = 0.379$, $t = 1.36$, *d.f.* = 11, $P = 0.20$). At the migration flyway (the dune site) and at one of the feeding sites (the canal site), sonar calls were recorded for 7.3 h on average (SD = 0.8, $n = 13$) throughout the night, and there were no significant differences between these two sites (Wilcoxon test, $W = 11.5$, $P = 0.24$). For other study sites, sample sizes were too low to be considered representative and due to low activity of bats the sonar calls were usually not recorded in late hours of night. At the forest site 2, the meadow site 2 and the marsh site, the bats were recorded for 6.9 (SD = 1.0, $n = 4$), 6.5 (SD = 0.2, $n = 2$) and 6.2 (SD = 1.2, $n = 4$) h on average, respectively.

The activity of *P. nathusii* was significantly higher at the dune site and the canal site than at the other sites (K-W test, $\chi^2 = 163.3$, *d.f.* = 6, $P < 0.001$). The frequency of feeding attempts also differed significantly among the sites (K-W test, $\chi^2 = 65.6$, *d.f.* = 6, $P < 0.001$), being highest at the dune site and the canal site (Table 1).

At the dune site, the recorded activity varied considerably from night to night, but within each night, the activity typically increased before midnight and then decreased again until sunrise (Fig. 2a). Of all the five-minute sections that contained echolocation calls ($n = 860$) from the site, 51.4% included feeding buzzes (the mean probability that feeding attempts were recorded from a passing bat was 0.514). The fraction of sections containing feeding buzzes was uniformly distributed over the course of the night ($\chi^2 = 4.2$, *d.f.* = 6, $P = 0.65$). Hence, bats migrating over the dunes made feeding attempts with the same frequency throughout the night (Fig. 2b).

At forest sites 1 and 2, the maximum activity was registered during the first hour of the night and for forest site 1 changes in the feeding rate reflected this

TABLE 1. The time of the earliest recorded sonar calls of *P. nathusii* in the evening, the duration of sonar sequences and the number of five-minute sections containing feeding buzzes per hour at the study sites ($\bar{x} \pm$ SE, sample sizes in parentheses)

| Site	Time of the earliest sonar calls (min after sunset)	Duration of sonar sequences per hour (s)	Number of 5-min sections containing feeding buzzes per hour
Dune	54 ± 9 (19)	307.8 ± 52.4 (119)	3.7 ± 0.4 (119)
Forest 1	43 ± 14 (13)	49.4 ± 10.2 (94)	1.2 ± 0.2 (94)
Forest 2	49 ± 10 (13)	5.5 ± 1.0 (99)	0.3 ± 0.1 (99)
Meadow 1	82 ± 10 (11)	37.6 ± 6.8 (84)	1.2 ± 0.2 (84)
Meadow 2	86 ± 20 (12)	36.0 ± 7.0 (78)	1.0 ± 0.2 (78)
Canal	59 ± 6 (8)	128.3 ± 24.4 (63)	2.6 ± 0.3 (63)
Marsh 1	06 ± 18 (12)	36.5 ± 8.0 (90)	1.0 ± 0.2 (90)
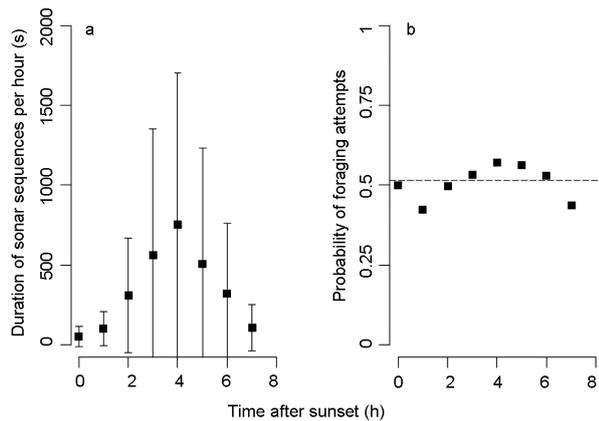
FIG. 2. Mean durations (± SD) of recorded sonar sequences of *P. nathusii* per hour (a) and the probability of feeding attempts (b) at the dune site — the migration flyway (the dashed line indicates the mean probability). 0 on the abscissa accounts for the sunset hour

pattern (Fig. 3a–b). At the forest site 1, 27.9% of the sections ($n = 409$) contained feeding buzzes. The highest proportion of sections containing feeding buzzes was recorded during the first hour of night and later on the probability for a passing bat to feed was significantly lower than expected according to a uniform distribution ($\chi^2 = 52.3$, *d.f.* = 6, $P < 0.001$). However, no significant deviation from a uniform distribution was found for the forest site 2 ($\chi^2 = 7.5$, *d.f.* = 6, $P = 0.28$), where 18.7% of all sections ($n = 134$) contained feeding buzzes.

At meadow sites 1 and 2, maximum activity was usually recorded around midnight (Fig. 3c). For the meadow site 1, 28.2% of all sections ($n = 362$) contained feeding buzzes. No significant deviation from a uniform distribution was found ($\chi^2 = 6.0$, *d.f.* = 6, $P = 0.42$ — Fig. 3d). For the meadow site 2, 28.7% of all sections ($n = 279$) contained feeding buzzes. Deviation from a uniform distribution was almost significant ($\chi^2 = 12.4$, *d.f.* = 6, $P = 0.055$). In this case, the fraction of sections containing feeding buzzes was highest during the second hour after sunset while the lowest feeding intensity occurred during the sixth hour after sunset.

At the canal site and the marsh site, activity peaks were observed at mid- and late night (Fig. 3e). For the canal site, 44.6% of all sections ($n = 368$) contained feeding buzzes compared to 34.9% ($n = 261$) for the marsh site. At both sites, the number of sections containing feeding buzzes were uniformly distributed throughout the night (the canal site: $\chi^2 = 10.1$, *d.f.* = 6, $P = 0.12$; the marsh site: $\chi^2 = 6.6$, *d.f.* = 6, $P = 0.36$).

DISCUSSION

The results agree with the hypothesis that *P. nathusii* uses a fly-and-forage migration strategy when migrating south along the Baltic coastline. On the migration flyway at the dune site, the mean probability of a passing bat to interrupt its flight and feed on available insects was 0.514 and did not change significantly over the course of the night. This also suggests that the flying insect abundance was always sufficient to permit energetically profitable foraging by the migrating bats. This situation may be different from that prevailing during spring migration, when the nights often are colder and insects are generally less active (Taylor, 1963; Avery, 1985; Rydell, 1989).

Generally, insectivorous bats are able to fuel their flight by ingested nutrients from consumed insect prey (Voigt *et al.*, 2010), but fat reserves may be used when insect prey is not available (Voigt *et al.*, 2012b). Energy accumulation is accelerated by reduced energy expenditure through the use of torpor (Carpenter and Hixon, 1988; Speakman and Rowland, 1999; McGuire *et al.*, 2009), which may be an advantage during migration — 'torpor assisted migration' (McGuire *et al.*, 2011). In contrast, most migratory birds spend a greater part of the journey on fuelling before non-stop flights or refuelling during stopovers (Schaub *et al.*, 2001; Lindström, 2003). Similarly bats have been suspected to consume body fat stores during migration (Thomas and Suthers, 1970; O'Shea, 1976) and refuel during stopovers (Fleming and Eby, 2003; Hedenström, 2009; McGuire and Guglielmo, 2009). However, the capability to use body fat stores at a high rate is limited in mammals, and, therefore, carbohydrates and proteins are consumed instead (Roberts *et al.*, 1996; McGuire and Guglielmo, 2009; Guglielmo, 2010). Migrating *Lasionycteris noctivagans* (silver-haired bats) have been observed to use short stopovers, lasting for one or two days, before crossing lake Ontario in Canada on their way south (McGuire *et al.*, 2011). A similar behaviour of migrating bats of several species has been observed at peninsulas and islands in southern Scandinavia (Ahlén *et al.*, 2009). The fly-and-forage strategy observed in *P. nathusii* and the stopover strategy observed in some other species do not necessarily indicate that the species have different strategies. Due to mammalian physiology and the ability to use daily torpor for energy accumulation, migrating bats probably apply a stopover strategy only in extreme cases, such as in front of major barriers, but otherwise feed on the
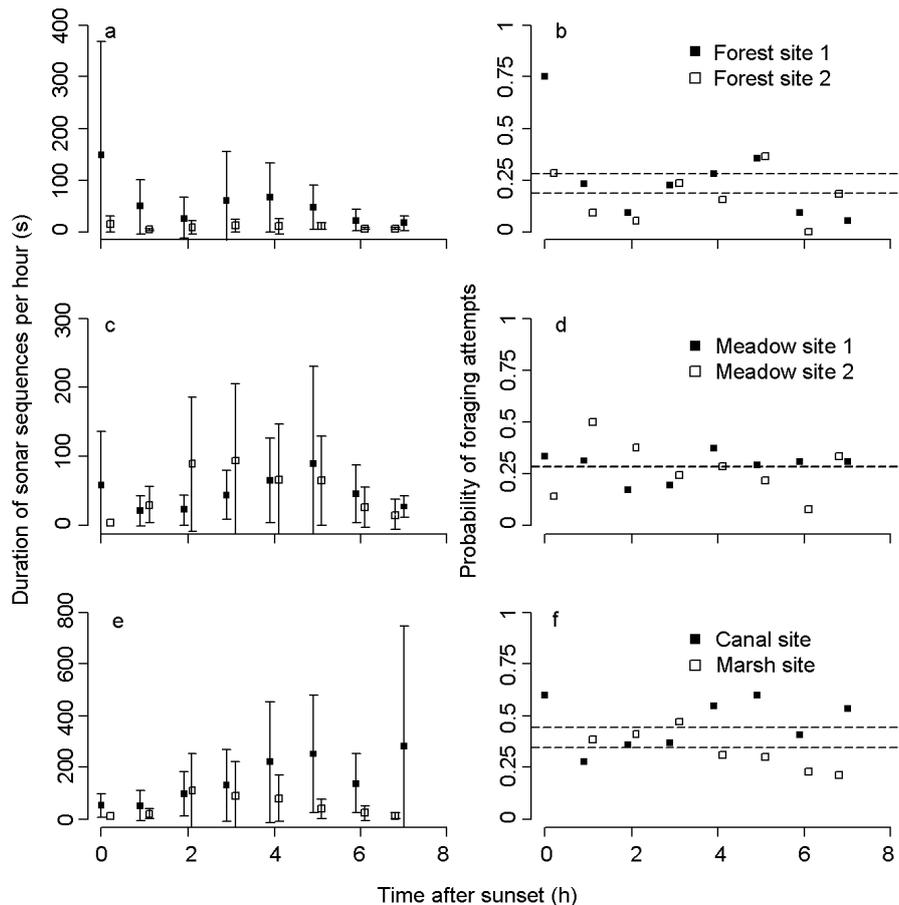
FIG. 3. Mean durations (± SD) of recorded sonar sequences of *P. nathusii* per hour (a, c, e) and the probability of feeding attempts (b, d, f) at studied forest sites (a, b), meadow sites (c, d) and wetland sites (e, f). The dashed line indicates the mean probability. 0 on the abscissa account for the sunset hour

wing, at least as long as the weather and insect availability permit.

The knowledge of habitat use during migration is of particular importance in environmental impact assessments of wind turbine power plants (e.g., Kunz *et al*., 2007), motorways (Gaisler *et al*., 2009) and other major exploitation projects (Rydell *et al*. 2010). In our study, feeding buzzes of *P. nathusii* were more frequently recorded in wetland habitats than in the meadow and forest habitats. This probably relates to the frequent emergence of non-biting midges (Diptera: Chironomidae) and other small insects associated with shallow water. Wetlands are frequently preferred as feeding habitats by *P. nathusii* (Ciechanowski *et al*., 2009; Flaquer *et al*., 2009) and other *Pipistrellus* species (Racey and Swift, 1985) and this also applies to our case.

Each night the first sonar calls of *P. nathusii* were typically recorded in *P. sylvestris* woodland habitats some 40–50 minutes after sunset; these woodlands were probably used as roosting habitats. The presence of trees facilitates the exploitation of flies and other insects that swarm at dusk, because they provide the bats with protection from raptorial birds that may still be active at that time. Open tree-less areas are typically avoided by aerial-hawking bats early in the evening (Rydell *et al*., 1996). At the two forest sites, the feeding rate was lower than at the other study sites and the maximum feeding rate was recorded during the first hour after sunset, which most likely corresponded to the peak activity in small flies (Rydell *et al*., 1996). During the later hours, the feeding rate decreased and remained relatively low, suggesting a decline in aerial insect availability (Lundy *et al*., 2012). Therefore the importance of pine forests as feeding habitats for *P. nathusii* during the migration flights may be relatively low, compared to wetland habitats, for example, but woodland habitats still need to be considered as potential roosting habitats.

Woodland edge habitats are normally used more intensively by bats than core-habitats (Hein *et al.*, 2009), which was supported by our observations at forest sites 1 and 2. Edges of continuous woodlands may be used as migration corridors in the same way as rivers (Furmankiewicz and Kucharska, 2009) and other linear landscape elements (Verboom and Huitema, 1997). This problem needs to be addressed in future research, so that essential migration corridors for bats can be identified and protected.

The results of this study can be referred mainly to low-altitude migration flight, because ultrasound detectors used in this study are able to record the sonar calls over relatively short distances (20–50 m in *P. nathusii*). However, migrating bats may presumably fly higher as well.

We conclude that during autumn migration individual *P. nathusii* apply a fly-and-forage strategy throughout the night as long as the aerial insect availability is high enough to provide profitable feeding. A stopover strategy may be used in other cases such as, for example, when autumn migration coincides with mating (Lundberg, 1989). In future research, nocturnal time budgets of individual bats during migration should be investigated using satellite tracking (e.g., Trierweiler *et al.*, 2007; Holland and Wikelski, 2009; Strandberg *et al.*, 2009) or small radio transmitters tracked from the ground or from aircraft (Parsons and Jones, 2003; Holland *et al.*, 2006).

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