Foraging range and habitat use by Aquatic Warblers *Acrocephalus paludicola* during a fall migration stopover

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Abstract. Stopover sites of migratory songbirds are of great importance in the context of the maintenance of a species migration strategy. Here we studied the spatial needs and habitat selection of the endangered Aquatic Warbler at a major migration stopover site in France, the nature reserve of the Seine estuary. We radio-tracked 15 migrant birds in August 2008 to study habitat use and selection at that stopover site, and analysed faeces and blow trap samples to determine the local diet of the species and to compare food availability among the different available habitats in the reserve. Range size was estimated with fixed kernels and was on average 9 ha (90% isopleths), with daily core ranges (50% isopleths) of just over 1 ha. There was no variation in range size or habitat use during the survey period (August) or during an individual stopover stay. Studying habitat selection within the modelled ranges, we found that the species displayed a preference for wet grassland habitats. Larger daily ranges included more reedbed and fewer grassland areas. This matches the habitat preferences known from breeding and wintering grounds. The main identified prey belonged to a few invertebrate orders, with Odonata, Lepidoptera, Coleoptera and Araneida making the largest contributions to the biomass consumed. There was no significant difference in invertebrate availability between grassland and reedbed habitats in the study area. The availability of grassland habitats close to the reedbeds appears to be a key parameter to ensure the rapid and efficient refuelling of migrant Aquatic Warblers during their autumn migration.

Key words: *Acrocephalus paludicola*, fixed kernel, habitat selection, diet, tracking, wet grasslands

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INTRODUCTION

Long-distance migration requires exceptional energetic reserves, and migratory songbirds must rest and deposit fat reserves at stopover sites while travelling between breeding and wintering grounds. In songbirds, most of the migration period is spent at stopover sites. As a consequence, understanding the impact of environmental changes such as habitat loss or fragmentation along the migratory routes is essential for efficient conservation planning (Huotto 1998). The vital importance of migration stopover sites to en route songbirds has come to the forefront of avian conservation (Petit 2000). The Aquatic Warbler *Acrocephalus paludicola* is Europe’s most threatened migratory songbird, as it has declined dramatically over the last century largely because of the drainage of its wetland breeding habitats. Much of its former habitat has been transformed and lost during the last century, especially in the Western part of its range (Birdlife International 2009). Its global population is estimated at 10,500–14,200 singing males. Most birds use a western migration route in autumn, with large numbers visiting French coastal marshes mainly in August (Julliard et al. 2006). During migration, Aquatic Warblers had been reported to strongly favour low stands of sedges and reeds near open water, normally along rivers, estuaries and coastal lagoons (de By 1990). However, these habitat preferences can be challenged when considering the similarity of habitats used by the species on its breeding and wintering areas, where it forages in wet grassland habitat types (Salewski et al. 2009). The identification of high-priority stopover sites and of stopover habitats critical to the long-term persistence of the migratory strategy are necessary to implement comprehensive conservation schemes (Yong et al. 1998, Petit 2000). In France, many
important stopover sites have been identified (Julliard et al. 2006), yet concrete habitat use and selection on such refuelling sites has to be studied (Bargain 2002). In this context, we radio-tagged migrant Aquatic Warblers at one major stopover site in northern France, the Seine estuary, in order to determine the spatial needs and the use of available habitats by refuelling birds. With the aim to improve our knowledge of the species foraging habitat selection, we also implemented a field sampling of invertebrates available for the warblers within the different habitats found close to the ringing stations. We further analysed faeces collected from migrant warblers on the site and compared the availability of those preys detected in faecal samples within the different habitats used on stopover.

**METHODS**

**Study area and radiotagging**

The study was conducted in the Nature Reserve of the Seine estuary, just south of Le Havre city, department of Seine-Maritime, in northern France. This is the northern shore of the estuary of the Seine river (49°27’N 0°20’E) covered by large reedbeds flooded during highest tides over an area of 30 km². The study area is part of a Nature Reserve which holds numerous (more than 200) hunting lodges, managed within the reedbeds as mostly rounded patches centred on small ponds surrounded by a belt of grass covers, parts of the reedbed being mowed. This is a renowned stopover site for the Aquatic Warbler, where for example 110 individuals were caught in August 2009 during dedicated ringing operations. The birds studied in this paper have been captured there in August 2008 following a national standardized ringing protocol (with mist-nets and tape-luring from dawn onwards; CRBPO 2010). Birds were tagged with tail-mounted radio-transmitters (Small PIP3 single celled tag by Biotrack Ltd, UK, weighting 0.35g, thus representing on average 3% of the body mass of the bird — on average 11–12 g for Aquatic Warblers stopping in France).

**Sampling scheme**

Warblers were tracked using FT817 ND Yaesu receivers and a 4-element FX-205V antenna. Bird tracking was carried daily by two persons out by walking within the reedbed and around the lodges. We plotted the geographical position of each location with an estimated precision of c. 5 to 10 m on 1 : 25 000 aerial photographs. Once radio-tagged, each warbler was tracked daily during one to five days (see Table 1), in order to obtain multiple regular locations for each individual. Birds were tracked during 5 hours in the morning (7:00 to 12:00 am) then again during 4 hours in the evening (from 6:00 to 10:00 pm). The minimum interval between successive locations of a single bird was 15 minutes. The available sample locations per day per individual were 25 ± 10 (range 5–46). After this intensive tracking period, the area was just checked for a single daily contact, in order to verify if the individual was still present or if it left the site during the night before. We thus have for each individual, a date of capture and tagging, and a date of apparent departure from the stop-over site (see Table 1).

**Home-range estimates**

Home-ranges were estimated using the Animal Movement extension for ARCVIEW GIS 3.2. We used Fixed Kernel methods (FK) with least squares cross-validation (Seaman & Powell 1996); 90% isopleths (FK90) were taken as total range estimates and 50% isopleths (FK50) as intensive-use-area estimates. For each individual, we estimated a global range for the whole tracking period, and daily ranges for each day it was tracked. These estimates were also calculated after excluding surfaces covered by open water which is obviously a non-foraging habitat.

**Habitat use**

A land cover map was created as a GIS layer from aerial photographic material completed with field verifications. Three different habitat categories were considered: open water, reedbeds (*Phragmites* and *Scirpus* reeds), and wet grasslands (including fen mires dominated by herbs, pond surrounds, humid grass tracks). This layer was further superimposed to the bird ranges (either global or daily, either 90% or 50% isopleths) to determine the habitat use within the ranges. The proportion of each habitat type within each individual stop-over range was estimated (for global and daily individual ranges). Principal Component Analyses were then conducted on these proportions to plot eventual differences in habitat use between individual ranges. PCAs were conducted for FK90 and FK50 ranges, though results of PCAs are presented below for the FK90 ranges, as results for the FK50 ranges were very similar. In the Principal Components Analysis performed
on global FK90 ranges, the first two PC axes captured 93.0% and 6.5% of variance, respectively. The first PC axis (PC1 on Fig. 2) was positively related to the proportion of wet grasslands (0.708) but negatively to the proportion of reedbed (-0.706), while PC2 was negatively correlated with reedbeds (-0.489) and wet grasslands (-0.500) but positively to open water (0.715). A Principal Components Analysis was also performed on the daily FK90 ranges. The first two PC axes captured 96.0% and 3.4% of variance, respectively. PC1 was positively correlated to reedbed (0.689) and negatively to grass (-0.724). PC2 was positively related to reedbed (0.487) and grass (0.463) and negatively to open water (-0.741). A PCA performed on the FK50 ranges produced very similar results.

Habitat selection
The study area is covered by 66% of reedbed, 9% of wet grassy areas and 6% of open water — other not here studied land covers consist of tracks, lodges, shores. The habitat selection was studied using the electivity index of Jacobs (1974). For each habitat type h, the index $D_h$ was estimated as $D = (r - p)/(r + p - 2rp)$ where r is the proportion of the habitat within the stopover ranges, and p the proportion of the same habitat in the study area. The index varies from -1 to +1, and habitat electivity varies can be deduced from the index values as follows: strong avoidance (-1 < D < -0.5), moderate avoidance (-0.5 < D < -0.25), no preference (-0.25 < D < +0.25), moderate preference (+0.25 < D < +0.5), strong preference (+0.5 < D < +1).

Faecal analysis
The diet of the Aquatic Warblers while on stopover was assessed by faecal analysis. In August 2008, we collected 39 independent samples of faeces during ringing operations. We placed birds in special bags with a plastic-coated bottom, fifteen minutes before their release. When faeces were found in the bag after this short storage, they were collected and stored in alcohol. Faeces were further dissected under a binocular microscope. Identifiable chitinous fragments were counted in each sample with the aim to estimate the minimum number of individuals of each taxonomic group (e.g. four Odonota wings were counted as one individual).

Invertebrate sampling within habitats
We used 3 standardized coloured (yellow, white, blue) blow traps per station (for a total of 26 stations). The traps were placed on the ground and filled with an unattractive conservative liquid, in order to assess invertebrate density-activity on the ground. This semi-quantitative invertebrate sampling methodology is the one carried out in the European monitoring program ALARM (www.alarmproject.net/alarm/). We evaluated the abundance of the main invertebrates consumed by Aquatic Warblers among the two main habitat types present in the study area: reedbeds and wet grasslands. All sites were sampled simultaneously and at 4 time periods in August, and we collected 147 efficient samples on 26 stations. The traps were deployed for three days, when the captured invertebrates were collected, identified, dessicated and weighted (see Kerbiriou et al. 2010 for more details). For analysis we pooled the three blow traps per station. We retained the dessicated biomass as an estimate of invertebrate availability, considering either all taxa or only those whose rests had been found in faeces.

Statistical analyses
We used a linear model to look for potential effects of the sampling effort (as the number of available locations, or the number of successive days with tracking data), and the date of the last day with tracking data on the obtained estimates of stop-over range sizes. Variations in daily range size and composition were realized using linear mixed-effect models to test for the effect of the number of locations used to model the range, the date, the number of day before departure, with a random effect of the individual identity. We compared invertebrate availability between reedbeds and grasslands using ANOVAs, first controlling for the date of trap deployment (as a categorical variable, though considering it as a continuous variable did not change the results). We performed all statistical analyses using the R statistical software and the lme4 package for the mixed model (R Development Core Team 2008).

RESULTS

Range size variation
Stopover range size exhibited large variation between individuals, with a mean $\pm$ sd of 9.05 $\pm$ 11.04 ha (n = 15; range 0.48–42.5 ha, Table 1). The 50% isopleths ranges (FK50) represented 21–34% of the 90% isopleths ranges (FK90) (29% on average). Overall, the range size did not vary with the sampling effort or the tracking period.
For the 90% isopleth ranges, we found no significant effect of tracking duration (in days; \( t_{12} = 1.56, p = 0.14 \)) and of the date of last tracking day (\( t_{12} = 0.58, p = 0.57 \)); replacing the tracking duration by the number of locations (i.e. the plot sample size used to estimate the range) did not reveal a significant bias due to the sampling strategy (sample size, \( t_{12} = 0.56, p = 0.59 \); last tracking day, \( t_{12} = 0.04, p = 0.97 \)). Very similar results were found if considering the 50% isopleth ranges. A few examples of ranges are presented in Fig. 1.

### Daily range sizes

Daily range sizes averaged 4.24 ± 3.77 ha (range 0.03–17.5 ha) for the FK90, 1.25 ± 1.13 ha (range 0.01–4.98 ha) for the FK50. After adjusting the daily range size to the daily number of locations used to model (\( t_{11} = -0.61, p = 0.55 \)) and to the date of the tracking day (\( t_{11} = 1.04, p = 0.32 \)) in the mixed-effect model containing a random effect of the individual bird identity, we did not find a significant variation of daily range size with the number of days before the end of the stop-over (\( t_{11} = -1.22, p = 0.25 \)). We found very similar results if using the 50% isopleth daily ranges (number of days before the end of the stop-over, \( t_{11} = -1.32, p = 0.21 \)).

### Habitat use

The Fig. 2 plots the coordinates of the individual ranges along the first two principal components of the PCA performed on the FK90 ranges. Larger ranges are those including more open water (Pearson’s correlation between range size and coordinate along PC2 axis: \( r = 0.84, n = 15, p < 0.001 \)). Results obtained for the 50% isopleth ranges were very similar (Pearson’s correlation between coordinates of FK90 and FK50 ranges on first PC axis, \( r = 0.92 \); on second PC axis, \( r = -0.87 \)). If excluding surfaces of ranges made of open water, the mean ± sd FK90 global range size was 8.05 ± 9.50 ha (range 0.47–37.40; average ± sd was 5.95 ± 5.12 ha if excluding the largest range). Similarly, the FK50 ranges without open water covered 2.4 ± 2.7 ha (range 0.11–10.71; 1.76 ± 1.55 ha if excluding the largest range).

### Trends in daily habitat use

To test if the habitat use varied during the stop-over period, we performed a linear mixed-effect model to predict the coordinate of the individual daily range on the first PC axis performed on the FK90 daily ranges (so a reedbed–grassland axis) with the date and the number of days before the bird’s departure from the site, and first accounting for daily range size and with ‘individual’ as a random factor. Only the daily range size was significantly correlated with the PC1 coordinate for FK50 ranges (\( t_{30} = 2.31, p = 0.028 \)), which means that larger daily ranges included more reedbed and less grassland areas. We failed to find any temporal changes in habitat use within daily ranges, either during the migration period or during individual stopover duration.

### Table 1. Stop-over foraging range size of 15 Aquatic Warblers, as estimated by the 90% and 50% isopleths of the fixed kernel (FK).

Ranges are estimated for the whole period of individual survey, and we present the duration of survey (in days), the number of locations used for modelling as well as the day of capture and tagging for each individual.

<table>
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<tr>
<th>Bird</th>
<th>Range FK90 (in ha)</th>
<th>Range FK50 (in ha)</th>
<th>Duration of survey</th>
<th>Number of locations</th>
<th>Date of tagging</th>
<th>Date of last contact</th>
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<td>2</td>
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<td>4.04</td>
<td>1.10</td>
<td>5</td>
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<td>7</td>
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<tr>
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</table>
Habitat selection

We estimated the Jacobs' indices of habitat selection for the three habitat types and for the 15 individual global KF90 ranges. Only the wet grassy covers had a positive electivity index value ($D_{\text{grass}} = 0.37 \pm 0.15$) while the other two habitat types had negative index values revealing avoidance ($D_{\text{reedbed}} = -0.12 \pm 0.14$, $D_{\text{water}} = -0.99 \pm 0.01$). All indices significantly differed from similarly distributed data centred on zero as revealed by one sample t-tests (d.f. = 14; $D_{\text{grass}}$, $t = 9.3$, $p < 0.001$; $D_{\text{reedbed}}$, $t = -3.4$, $p = 0.004$; $D_{\text{water}}$, $t = -473$, $p < 0.001$).

Invertebrates in faeces

In the faecal samples, we recorded a total of 198 prey items (see Table 2). Few of them could be identified to species. Homoptera were mainly aphids (probably *Hyalopterus pruni*) and Diptera were mainly Brachyptera of medium to large species of Syrphidae or Dolichopodidae families. In terms of abundance, the diet of the Aquatic Warbler was dominated by Diptera and Aphids. When considering occurrence, groups such as Araneida, Heteroptera or Coleoptera were quite well represent. Using a predictive model of the relationship between body length and invertebrate group (Ganihar 1997), we estimated the...
biomass of each group. Odonata, Lepidoptera, Coleoptera and Araneida contributed more to the consumed biomass than Diptera or Homoptera.

**Invertebrates in reedbeds and grasslands**

We compared the invertebrate biomass in sampled reedbeds and grasslands. In a first analysis, all taxa were considered, and there was no significant difference in biomass between reedbeds (n = 34) and grasslands (n = 15), considering either total biomass ($F_{1,44} = 0.09$, $p = 0.76$) or only the taxonomic groups found in faecal samples ($F_{1,44} = 0.02$, $p = 0.88$). Considering the eventual mowed reedbeds (n = 11 samples) as a separate group did not change the results ($F_{2,43} = 0.45$, $p = 0.64$ for total biomass, $F_{2,43} = 0.33$, $p = 0.72$ for the restricted biomass).

<table>
<thead>
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<th>9</th>
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</tr>
<tr>
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</tr>
<tr>
<td>Odonata</td>
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<td>2</td>
<td>39</td>
</tr>
</tbody>
</table>

Table 2. Arthropod groups found in faecal samples of migrant Aquatic Warbler while on stopover: occurrence frequency (among all samples), proportions (in %) of total numbers and of total biomass.

**DISCUSSION**

**Habitat use**

Studies of ranging behaviour can provide valuable information on the ecological requirements of a species. They may be an essential tool in designing conservation policies (Sutherland 1998) as they provide the information needed to predict the consequences of land-use change on species’ habitat use, especially in regions subject to major habitat transformations. This is also true for stopover habitats where migrant birds stop while on migration in order to deposit fat and restore body reserves. In the Seine estuary, Aquatic Warblers on stopover forage within small global ranges of e.g. 9 hectares, concentrating in core ranges of less than 3 hectares, which is not a large area. Our results further clearly indicate that the species prefer to forage in wet grasslands compared to reedbeds. We did not find a significant variation in daily habitat use during the stop over duration of the tracked birds, while larger global ranges were those including more open water areas, so a larger amount of non-foraging habitats artificially increasing the global range size. Indeed, the foraging habitats — namely wet grasslands — selected by these stop-over migrants closely match some habitats used on breeding sites (Tanneberger et al. 2009, 2010), at the yet only known wintering site in Senegal (Salewski et al. 2009) and at another stopover site in Brittany, France (Bargain 2002). From these various evidences, the Aquatic Warbler uses wet grasslands and not pure and dense reedbeds as foraging habitats to breed, refuel and winter. Wet grasslands at stopover sites are however only small habitat patches, while breeding or wintering habitats cover thousands of hectares in flooding plains.

**Invertebrate availability**

Despite wet grasslands being identified as highly selected by the warblers, we failed to find a global difference in invertebrate abundance between such grasslands and various reedbed habitats across the study site. The average invertebrate biomass seems higher in grasslands, but the high variability of the biomass in reedbeds precludes finding statistical differences, considering either the global biomass or only those taxa effectively consumed by the species (here identified from faecal analyses, with Odonata, Lepidoptera, Coleoptera and Araneida contributing more to the consumed biomass). Most consumed invertebrates have a partly aquatic life cycle, explaining why the Aquatic Warbler forages in wet grasslands close to open water areas (see e.g. Fig. 1), while also microclimatic aspects may play a role by their function as guidance for arthropods towards edges. Interestingly, the preys identified at this stopover site are very similar taxonomically and in their large sizes to those identified at another French stopover site in Brittany (Kerbiriou et al. 2010) or consumed on breeding sites (Schulze-Hagen et al. 1989).

**Range sizes**

The stopover range sizes found here are similar or slightly smaller than those reported on breeding sites (Schaefer et al. 2000), though we used kernel estimators which generally produce more restricted estimates. An originality of our study is to focus on range size used for refuelling on stopover sites during migration. Chernetsov &
Titov (2001) studied the foraging movements of European Reed Acrocephalus scirpaceus and Sedge A. schoenobaenus Warblers at migratory stopover sites. They compared the frequency distribution of distances between capture and recapture localities of individual birds with a simulation model of a random distribution of movements. According to their results, the warblers move nearly randomly between localities at a stopover site, and have home ranges that are too large (3 to 5 hectares) to be exclusive territories at migratory stopovers. Bibby & Green (1981) reported the movements of a marked Reed Warbler in September in Portugal as restricted to 80 meters away from a fixed point during 150 minutes. This is not dissimilar to the daily core range found here for the Aquatic Warbler (FK50 daily range of 1.25 hectares). Overall, the literature hardly provides any estimate of stop-over range size for Acrocephalus warblers. The small stopover range size found for the Aquatic Warbler in the Seine estuary probably reflects the high refuelling capacity of the area, as birds concentrate mainly around hunting lodges where grassy habitats are also concentrated, while they could easily switch from a lodge to others. Stopover range size of radio-tracked Swainson’s Thrushes Catharus ustulatus was estimated at 1.9 hectares during fall migration in California (Tietz & Johnson 2007), which is very small. Interestingly, the approach adopted by these authors was very close to the one we implemented on the Aquatic Warbler: capture and radio-tracking of migrants, faecal analyses, and study of habitat use and selection with a further comparison of food availability between the different available habitats.

Conclusion

Concerning habitats and refueling resources for migrant birds at stopover sites, Ktitorov et al. (2008) suggested the existence of a threshold of landscape suitability: in sites with not enough suitable habitat cover, birds tend to lose body mass or to gain mass at a lower rate. The comparison of tracking data, habitat use and selection, stopover duration estimates (Schaub et al. 2001, Bachler & Schaub 2007) and body mass gains (Péron et al. 2007, Schaub et al. 2008) between different stopover sites along the autumn migration route of the species (Julliart et al. 2006) could further help with identifying the major refueling sites to be first preserved to ensure the long-term maintenance of the species specific migration strategy.

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References


STRESZCZENIE

[Wielkość arealu i wybiórczość siedliskowa wodniczki na miejscu przystankowym podczas wędrówki jesiennej]

Ptaki wędrujące na dalekie dystanse muszą zatrzymywać się na odpoczynek i żerowanie konieczne do kontynuowania przechodu. Takie miejsca przystankowe mają ogromne znaczenie dla ptaków, a rozpoznanie w tych miejscach preferowanych przez ptaki środowisk konieczne jest dla efektywnej strategii ochrony gatunków.

W pracy przedstawiono wyniki badań nad wybiorocznością środowisk i wielkością areałów wodniczki w ważnym dla tego gatunku miejscu przystankowym we Francji, w rezerwacie w ujściu Sekwany. W sierpniu 2008 schwytano 15 osobników, którym założono nadajniki telemetryczne. Każdego ptaka namierzano przez 1–5 dni (prace prowadzono przez pięć godzin przed południem i cztery wieczorem) a następnie raz dziennie, aby określić dokładną datę jego odlotu. Uzyskane w ten sposób miejsca lokalizacji wodniczek naniesiono na mapę siedliskową, na której wyróżniono trzcinowiska, wilgotne łaki i powierzchnię toni wodnej. Określono wielkość areałów (opisywaną w pracy dla 50% i 90% wszystkich lokalizacji danego osobnika), w powiązaniu z wykorzystywanymi siedliskami oraz wybioroczność środowiskową. Prócz tego w kałem złapanych ptaków poszukiwano dających się zidentyfikować fragmentów bezkręgowców stanowiących pokarm wodniczek, a także określano dostępność pożywienia w różnych środowiskach badanego miejsca przystankowego.

Średnia wielkość arealu wodniczek w całym badanym okresie pozostawania na miejscu przystankowym wynosiła ok. 9 ha i nie była zależna od liczby lokalizacji, czy daty odlotu ptaka (Tab. 1). Wzrost wielkości areałów związany był z udziałem otwartego toni wodnej (Fig. 2), zaś większe arealy dzienne zawierały więcej trzcinowiska i mniej wilgotnych łak — środowiska preferowanego przez wodniczkę na badanym terenie (Fig. 1). W kałe ptaków znaleziono resztki przypisane do 198 ofiar. W pokarmie dominowały muchówki i mszyce, jednak pod względem biomasy większe znaczenie miały ważki, motyle, chrząszcze i pająki (Tab. 2). Stwierdzono, że dostępność tych głównych grup bezkręgowców była podobna w trzcinowiskach i wilgotnych łakach.

Na podstawie uzyskanych wyników wydaje się, że dla wodniczki dostępność wilgotnych łak blisko trzcinowisk jest kluczowa dla szybkiego nabierania masy przed dalszą częścią wędrówki jesiennej.