Rijksuniversiteit Groningen

The influence of food abundance on the territorial behaviour of migratory songbirds during the winter residency

Wender Bil

Bachelor Thesis Life Sciences (WLS13)

Dr. J. Ouwehand

March 15, 2019

Contents

Abstract

Territoriality by means of competitor exclusion is a widespread spatial behaviour among migratory songbirds during the course of the non-breeding season. The fitness outcome of this behaviour is mainly determined by the ratio between the benefit of appropriating food sources and the costs imposed by territory defence. However, given the fact that natural changes in food abundance occur during the course of the non-breeding season, territorial songbirds will likely experience spatiotemporal shifts in the relative affordability of territorial behaviours. In order to understand this widespread spatial strategy despite the food-induced spatiotemporal shifts in its potential benefits, it is important to establish the existence of flexibility within the behaviours that constitute territoriality. In this paper I review the literature that addresses the influence of food abundance on 1) site fidelity, 2) territory size, and 3) territorial aggression during the non-breeding residency of territorial migratory songbirds. I found sparse evidence for changes in territorial behaviour as induced by changing food abundance. Of all components of territorial behaviour, the effect of food abundance on territory size was quantitively best explored, though no effect was found in study systems where territories were already established. Furthermore, evidence is found for food-related flexibility in territorial aggression: a behavioural change for which I suggest that it possibly precedes changes in spatial behaviour. Therefore, I recommend future studies on the subject to simultaneously focus on the different behavioural components of territoriality, in order to establish the existence of a hierarchy in flexible behavioural mechanisms that territorial migratory songbirds have at their disposal to cope with spatiotemporal shifts in food abundance.

1. Introduction

The planetary phenomenon of photoperiodic seasonality forms the basis of large-scale spatiotemporal fluctuations in vital resources for organisms around the globe. Due to their flying capacity birds are well suited to track these resources over fast distances, promoting highly mobile strategies to utilize seasonally suitable habitats. Generally such migratory strategies involve segregated reproductive and non-reproductive sites which are separated by tens, hundreds or even thousands of kilometres (Newton, 2008). In most migratory songbirds the breeding areas are positioned on higher latitudes during the Northern hemisphere spring and summer, while in autumn these species will migrate to lower latitudes during the non-breeding season (Newton, 2008), (hereafter also referred to as 'the wintering season').

The physiological demands during the breeding and non-breeding period are often very different in migratory birds. In many species the breeding semester is a tightly scheduled period with several life-cycle events, often comprising one or multiple reproductive bouts, post nuptial moult and pre-migration fuelling, that altogether incur high physiological demands (Drent & Daan, 1980). During the non-breeding residency there are usually less events at play. However, individual fitness outcomes in migratory songbirds are found to be strongly influenced by behavioural decisions during the non-breeding season. First of all, it is a necessity for non-breeding songbirds to assimilate enough food to survive until the next breeding season. Additionally, individual site selection influences the risk of predation during the period of residency (e.g. Cuadrado, 1997).

Next to these direct survival effects there is also accumulating evidence for fitness consequences of non-breeding behaviour on future life-stages. For example, mate selection is found to be influenced by wintering conditions in species that acquire condition-dependent plumage traits during moult on the wintering grounds (Saino *et al.*, 2004; Järvistö *et al.*, 2016). Additionally, non-breeding habitat selection is associated with the prospect of future migration success, as based on its influence on physiological conditions prior to departure and survival rates between successive winter periods (Marra & Holmes, 2012). Also the timing of migration is found to be affected by non-breeding site selection in songbirds (Studds & Marra, 2005), which in turn strongly affects individual reproductive outcome (Norris *et al.*, 2003). So, especially when winter resources are limited, wintering conditions are likely of big importance on the individual fitness outcomes in migratory songbirds.

Given the fitness consequences of non-breeding decisions one can expect songbirds to adjust their behaviour in favour of the most affordable strategy at their disposal (Davies & Houston, 1981). As most songbird species are subjected to spatiotemporal changes in wintering resources, various intra- and interspecific behavioural strategies have evolved in order to utilize resource changes (Greenberg & Salewski, 2005). In general this yields interspecific differences where the wintering behaviour of specialist species that feed on temporarily available food sources (e.g. frugivores and nectivores) is highly iterant, whereas generalists and species with relatively stable food sources tend to show longer stationary periods (Levey & Stiles, 1992; Greenberg, 1995). These stationary spatial strategies are typically accompanied with territorial behaviour, where individuals occupy a patch which they aggressively defend against competitors (Greenberg & Salewski, 2005).

The ultimate function of winter territoriality in songbirds is established as insuring food intake to optimize fitness perspectives (Hixon, 1980; Davies & Houston, 1981). The resulting site fidelity has the additional advantage of enabling birds to build up local knowledge, hence creating the opportunity to optimize site use in terms of food exploitation and predator avoidance (Beletsky & Orians, 1989; Cuadrado, 1997). This personal information is also found to be advantageous during contests against conspecific intruders (Beletsky & Orians, 1989; Tobias, 1997). However, territory owners also have to

guard and defend the territory, which goes at the expense of fitness enhancing resources like energy and foraging time (Davies & Houston, 1981). Therefore, territoriality can be expected to exist solely on occasions where its benefits outweigh the costs.

Territoriality is observed in most migratory species during the full course of their non-breeding residency (Greenberg, 1995). However, as food abundance for songbirds naturally changes during the course of the non-breeding residency in both the tropics (Moreau, 1972; Greenberg, 1995; Sherry & Holmes, 1996; Sherry *et al.*, 2005) and temperate regions (Newton, 2008) most territorial songbirds are likely subjected to changes in the affordability of territorial behaviours. In order to understand this widespread spatial strategy despite the food-induced spatiotemporal shifts in its potential benefits, it is important to establish the existence of flexibility within the behaviours that constitute territoriality.

In this paper I will review the literature to answer the question: 'What is the influence of spatiotemporal fluctuations in food abundance on territoriality in migratory songbirds during the non-breeding residency?'. In analysing the literature I will differentiate between the following behavioural components of territoriality: 1) site fidelity, 2) territory size, and 3) territorial aggression. I hypothesize this respective sequence to broadly represent an increasing order of subjected flexibility associated with changes in food abundance.

In order to gather information on this topic I conducted a literature search by means of the online search engines Google Scholar and Web of Science, starting with the terms "TS=(territor* AND migra* AND bird) AND TS=(winter* OR non-breeding)". Subsequently I used references from the initial sources to explore further literature on the topic. In order to ward off non-related effects I only included studies on wintering songbirds that empirically measured the within-individual effect of spatiotemporal fluctuations in food abundance on one or more of the mentioned components of territoriality in this analysis. Moreover, by focussing on the winter-residency of migratory territorial songbirds I try to rule out confounding effects between breeding and non-breeding territoriality due to same site use; since winter territories are mainly concerned with feeding and individual sustenance (Davies & Houston, 1981), whereas breeding territories also serve other purposes (e.g. to attract mates and rear young) which alters the fitness interests of these lasting territories.

The results of the literature search are presented in section 2. where I describe the established effects of spatiotemporal fluctuations in food abundance for the different components of territoriality. In the following section (3.) I will elaborate further on these results, with a special emphasis on the potential underlying mechanisms and adaptive values of established behaviours. Furthermore, I will briefly summarize the main conclusions of this essay and outline the encountered knowledge gaps within the literature on this topic in section 4.

2. Results

In total, five journal articles were found that empirically assessed the influence of spatiotemporal food fluctuations on territoriality in migratory songbirds. Two studies covered the influence on site fidelity, against four studies on territory size, and only one study investigated the effect on territorial aggression. An effect of food abundance on the investigated variable was observed in three of these studies (Table 1).

Table 1 Study subjects and established effects of food abundance on different measures of territoriality.

Measure	Species	Response food abundance	Source
Site fidelity			
	Ovenbird	No	Brown & Sherry (2008)
	Northern Watertrush	Positive	Smith et al. (2011)
Territory size			
	Ovenbird	No	Brown & Sherry (2008)
	Hermit thrush	No	Brown & Long (2006)
	Hermit thrush	No	Diggs et al. (2011)
	Fieldfare	Positive	Tye (1986)
Territorial aggression			
	Pied Wagtail	Negative	Davies & Houston (1981)

2.1 Site fidelity

The effect of food abundance on territory site fidelity was described in two articles. Illustrative is the work of Smith *et al.* (2011) who conducted an observational study by tracking Northern Watertrushes (*Parkesia noveboracensis*) during two winter seasons in Puerto Rico. Their study site comprised patches of different moisture levels and associated forest types. The abundance of ground dwelling invertebrates (the main food source of Watertrushes in the area) was found to be positively correlated with the amount of moisture. Territories were however scattered over different forest types.

The research started during the second half of the dry season: signifying increasingly dryer conditions levels in all forest types during the course of the research, and causing overall food abundance to decline. This food change was associated with the replacement of territories within the research area, following a pattern where abandoned territories were characterized by poorer food conditions than the territories after movement (Fig. 1) (Smith *et al.*, 2011).

Brown & Sherry (2008) also studied site fidelity in relation to experimental food manipulations in Ovenbirds (*Seiurus aurocapilla*) over the course of four wintering seasons in Jamaica, where Ovenbirds were found to exhibit both resident and floater behaviour. The diet consisted mainly (~60%) of ants, hence the food manipulation focused on changing the abundance of ants within territories. This was done both by locally annihilating ant colonies by means of insecticide, and increasing food availability by depositing ant-attracting fruits within territories. However, site fidelity was found to be unaltered by the treatments (Brown & Sherry, 2008).

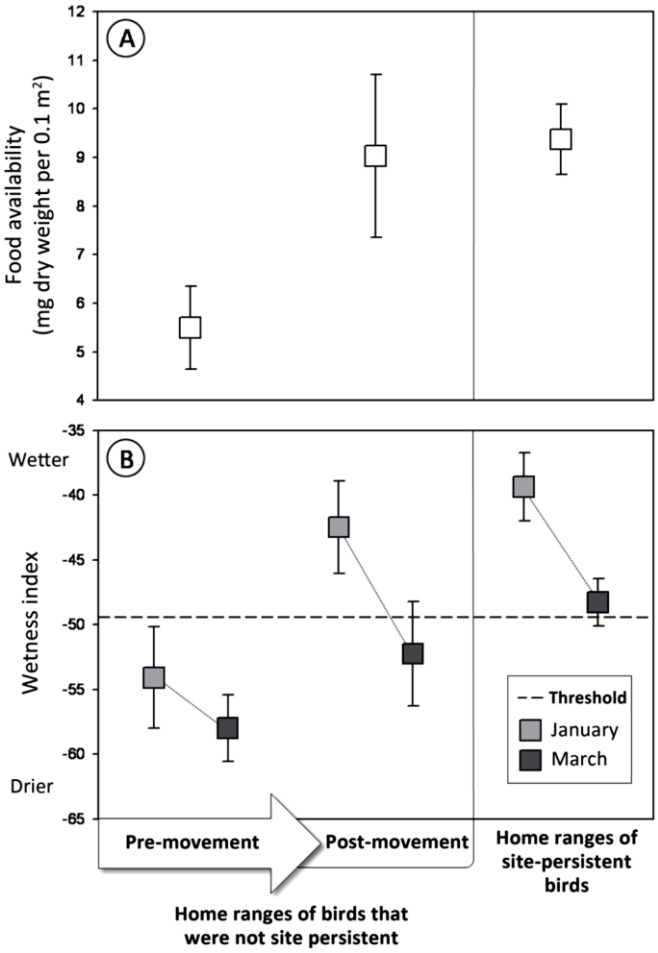

Figure 1 Food availability and wetness index for territories of Northern Watertrushes of both displacing and site-persistent birds. The wetness index was found to be strongly correlated with food availability. From: Smith *et al.* (2011).

2.2 Territory size

Several experimental studies have focussed on the influence of food abundance on territory size. Contrary to their expectations, the already mentioned study of Brown & Sherry (2008) found no effect of experimental food manipulation on territory size in Ovenbirds. However, sedentary birds tended to concentrate their activities around sites where food was supplemented. Moreover, it was found that Ovenbird densities correlated positively with the experimental supply of food. Since sedentary birds were not found to leave their initial home ranges, this change is attributed to the movement of floaters in accordance to food supply within the area.

Another experimental study on the effect of food abundance on territory size was conducted by Brown & Long (2006). Their study system concerned Hermit Trushes (*Catharus guttatus*) that wintered in Louisiana, USA, where individual territories were occupied for the course of the non-breeding season. The Trushes' diet consisted mainly of arthropod prey, though during periods of declined arthropod availability they showed a tendency to include fruit in their diet. The experiment consisted of reducing this food source by clearing out fruiting trees from territories. Subsequent radiotracking also revealed no difference in territory size as induced by the treatment (Brown & Long, 2006).

In contrast to the previous findings, Tye (1986) did establish an influence of food abundance on territory size in winter Fieldfares (*Turdus pilaris*). This study took place in England, in an area where Fieldfares were naturally found to only temporarily defend single food pieces (apples) against conspecifics and

other competitors. However, the territorial behaviours of Fieldfares extended to larger patches when subjected to experimentally created food clusters. Once this experimental supplementing stopped and food sources were depleted, the territorial birds were found to reside to their usual (non-territorial) behaviour (Tye, 1986).

2.3 Territorial aggression

Beside the studies on the spatial behaviour of territorial songbirds, only the study of Davies & Houston (1981) investigated the effect of changing food abundance on territorial aggression during the non-breeding season. Their study population concerned Pied Wagtails (*Motacilla alba*) that occupied winter territories along the River Thames in England, where they foraged on insects that washed upon the river banks. Territories where predominantly occupied and aggressively defended by adult males, that however sometimes tolerated juvenile subordinates within their range.

In order to provide insight into the effect of food abundance on this tolerant behaviour Davies & Houston (1981) investigated the supply and depletion rates of food sources within territories. The studied Wagtails fed solely upon insects along the water line that were supplied by the wave motion that moved insects both on shore and into the river again. This yielded a pattern where food abundance on a foraging stretch after full depletion first increased, and then (after the duration of about an hour) levelled off to a more or less stable quantity (Davies & Houston, 1981). Therefore, the individual feeding rate was found to be strongly influenced by the time since a stretch was last depleted. Besides the food abundance and its rate of renewal differed between days, which also influenced feeding rates. Altogether the equation for the feeding rate (number of obtained food items per minute), *F*, was represented by Davies & Houston (1981) as:

$$F = k(1 - e^{-bR}) \qquad \text{(Eq. 1)}$$

where maximum feeding rates and food renewal rates are represented by the parameters *k* and *b*. Individual birds were found to increase their feeding rates, *R*, by displacing their feeding activities within their territory in a systematic way by which they seemingly optimized the available food sources at the moment of visiting (and hence feeding rates, *F*).

In case of shared territories the individual time between visits stayed similar, but individuals tended to alternate their visits in a way that on average halved *R* for the territory owner (Davies & Houston, 1981). However, Davies & Houston (1981) also observed benefits of the presence of subordinate for territory owners, as subordinates also participated in territory defence: thereby lowering the costs of expelling intruders for the territory owner. In fact subordinates were observed to conclude with about half of the territorial conflicts themselves. Moreover, the detection probability increased due to the fact that both birds watched over different parts of the territory. This also resulted in a lower depletion time by intruders, and hence significantly lowered the time cost per intrustion for territory owners that tollerated subordinates. The observed foraging rate of a territory owner that shares its territory with a subordinate therefore matched the predictions from the equation:

$$F_s = \left[1 - \frac{1}{2}.T_s.N(k)\right].k(1 - e^{-bR/2}) \qquad \text{(Eq. 2)}$$

where *T* is the average time lost per intruder, which Davies & Houston (1981) expressed as a function of the detection probability and the time cost of foraging on sites that are depleted by undetected intruders, plus the average time spend on expelling an intruder once detected. As it was found that the number of intruders, *N*, was dependent on food abundance it is expressed as a function of *k*. Whereas feeding rates of single territory owners is given as:

$$F_0 = [1-.T_0.N(k)].k(1-e^{-bR}) \quad \text{(Eq. 3)}$$

Altogether, the study of Davies & Houston (1981) showed that Pied wagtails increased their feeding rates by exhibiting less territorial aggression towards single subordinates during periods of higher food abundance (Fig. 2).

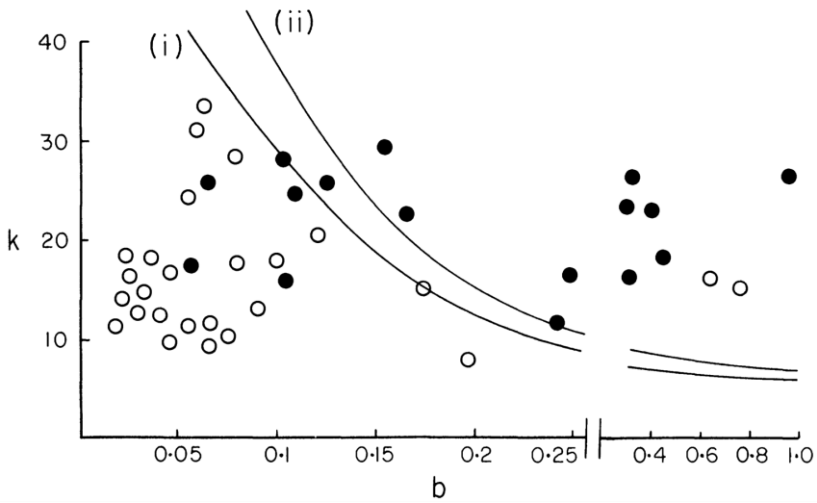

Figure 2 Observed resource renewal rates (b) and maximum feeding rates (k) for days when territory owners were alone (open dots) and when they tolerated subordinates (black dots). The lines show the theoretical division where foraging rates for both strategies equal each other based on the described formulas, when subordinates account for half (i) or a third (ii) of the territory defence. From: Davies & Houston, (1981).

3. Discussion

In total five journal articles were found that empirically assessed the influence of spatiotemporal food fluctuations on territoriality in migratory songbirds. Behavioural changes associated with shifts in food abundance were found within all investigated components of territoriality (site fidelity, territory size and territorial aggression). As the limited studies were unevenly distributed over these behavioural components and did not simultaneously cover the influence of food abundance on changes within these behaviours, the existence of an overall hierarchy of flexibility in territorial behaviour remains unexplored. However, the literature on these individual behavioural components provide some insight into the specific behaviour flexibility that songbirds have at their disposal in order to respond to shifting food abundance.

3.1 Site fidelity

Site fidelity was found to be positively correlated with food abundance in the Northern Watertrush study system of Smith *et al.* (2011), where territories with the lowest food abundance had a higher chance of being abandoned during the course of the season. Smith *et al.* (2011) mentioned that after moving out, these owners established new territories in habitat of higher quality than the initial sites. Though this upgrading of fitness perspective seems like an adaptive strategy, it also raises the question why these birds settled in territories of seemingly inferior quality in the first place.

I suggest two theoretical hypotheses for this behaviour. Firstly, the average fitness benefits of settlement might outgrow the costs of further prospecting (e.g. predation risk, conflicts with territorial birds) at a point where the individually sampled habitat is prone to sampling error. For example, when overall spatial food conditions are badly perceptible and thereby restricting the scope of prospecting, naïve birds might settle on optimal locations within relatively small areas of exploration. The upgrading pattern can subsequently arise when not all high quality habitats are occupied and the part of the population that ended up in the poorest territories are forced to leave their territory once food conditions deteriorate, and search for locations with higher food abundance outside their initial search area (see also Cresswell, 2014).

Another explanation might be that the spatial distribution of optimal settlement locations changes through time. In this case intraspecific differences in the movement of territories might result from the occurrence of both stable and unstable sites in terms of temporal habitat quality. Territory upgrading might thereby arise in the part of the population that inhabit unstable habitats, once they are forced to search for locations with higher food abundance when habitat quality begins to deteriorate.

Smith *et al.* (2011) mentioned that with the progressing of the winter season, birds directionally moved from the most desiccated locations towards areas that were initially inundated but started to dry up at the time of settlement. Since Watertrushes depend on solid soil for foraging (with techniques that includes leaf-tossing) it is clear that inundated areas offer no access to possible food sources. However, once the surface water dries up the emerging soil offers better foraging opportunities then the initially drier places in the surroundings. This supports the hypothesis that territory movements in Watertrushes are caused by the temporal change in the spatial distribution of optimal settlement habitat. Moreover it was found in this study that individuals used the same sites and showed the same directional moves within two subsequent wintering seasons (Smith *et al.*, 2011). This is also counterproof of the first hypothesis whereby these movements are the result of restricted local knowledge.

Contrary to the previous study, Brown & Sherry (2008) found no effect of food abundance on territory site fidelity in Ovenbirds. A possible explanations for this difference is that the reduced food supply was still sufficient to make its territorial occupation affordable. Additionally the threshold for abandoning a

territory could be lower compared to the same behaviour in the study of Smith *et al.* (2011), as this will likely result in a further reduction of fitness perspectives, due to the fact that suitable habitat was already saturated by territorial conspecifics (also see below), whereas in the study of Smith *et al.* (2011) abandoning a territory poor in food generally resulted in an upgrade.

3.2 Territory size

Though territory size is well known to be affected by the abundance of food (Stenger, 1958; Wilson, 1975), only Tye (1986) established an effect of food abundance on shifting territory dimensions. The fact that the other studies did not find an effect is most likely due to the different moment of territory establishment relative to their observations; Brown & Long (2006), Brown & Sherry (2008) and Diggs *et al.* (2011) all conducted their research in a period when territories were already established, and patches with suitable habitat were likely saturated with contiguous territories by then. This was also evident from the occurrence of floaters in these study areas.

As described by Hixon (1980) the size of such contiguous territories is likely constraint by the borders of surrounding territories, resulting in a point where territory size has to be compromised despite the fact that reaching the non-contiguous optimum might require further expansion (Fig. 3). The absence of a response in the above mentioned studies is likely mediated by this phenomenon, where the compromising point was already established based on natural conditions during settlement, and therefore the reduction in food abundance resulted in no clear size difference.

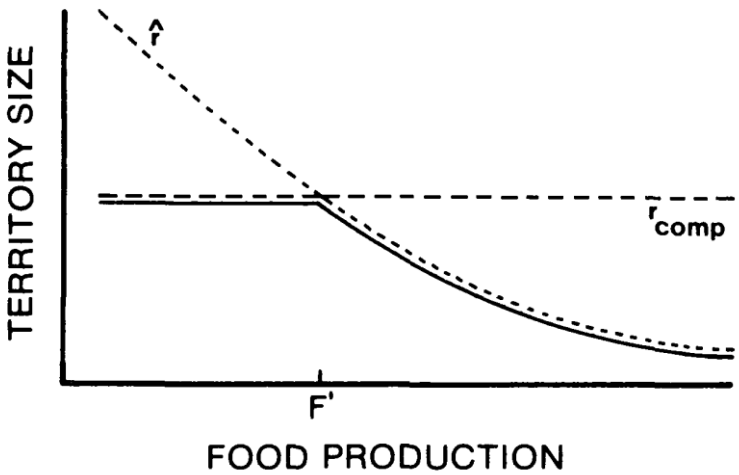

Figure 3 Optimal non-contiguous territory size ($\hat{r}$) in relation to local food production. In case of interactions with contiguous neighbours territory size may be forced to contract to a compressed state (r_{comp}) causing territory size to stay unchanged when food production drops below *F'* even though an expansion is required in order to reach optimal (non-contiguous) size. From: Hixon, (1980).

Contrary to the previous studies, Tye (1986) induced the establishment of territories within unoccupied areas, which likely caused his divergent findings. However, the statement of Tye (1986) that artificially induced territories were larger than the natural occurring territories seems contradictory in this sense, given the fact that more food was available during the experiment. However the mentioned 'natural territorial behaviour' was very short lived, and restricted to single food pieces: making it likely that these birds were not occupying territories, but appropriating single meals instead. Therefore, it is doubtful if (Tye, 1986) correctly attributed this behaviour to territoriality.

The finding of Brown & Sherry (2008) that territory size did not change in response to food supplementation requires further attention too, as food supplementation should theoretically result in a decreasing optimal territory size (Stenger, 1958; Wilson, 1975) which, in contrast to expansion, should

still be possible in a contiguous system. One explanation for the absence of this response could be that the overall food abundance was insufficiently supplemented to move the optimal territory size below the compromising point (Hixon, 1980). The described observation that the body condition of territorial birds improved as a result of supplementing (Brown & Sherry, 2008) supports this notion.

However, the additional observation that the density of conspecifics (most likely floaters according to Brown & Sherry, (2008)) in supplemented territories increased, points towards the possible existence of a preceding behavioural response which is more in accordance with the findings of Davies & Houston (1981), where aggressive behaviour is varying in response to changes in food supply. Unfortunately Brown & Sherry (2008) only studied territorial behaviour by means of telemetry patterns without actively measuring aggressive behaviour.

3.3 Territorial aggression

The study of Davies & Houston (1981) on Pied Wagtails was the only study found to empirically assess the influence of food abundance on territorial aggression. They established that under good food conditions territorial males tolerated subordinates in their territories that also participated in territory defence. This behaviour was explained by the fact that during these conditions foraging rates improved as a result of the shared territory defence (Davies & Houston, 1981). The fact that only physical subordinate females and juveniles were tolerated by these males, is likely caused by the fact that once food abundance decreased these birds were expelled from the territory again (Davies & Houston, 1981). This observation is in accordance with the resource holding potential hypothesis (Parker, 1974), which states that in general resident individuals are of higher intrinsic quality then other birds, and hence better able to dominate during intraspecific conflicts.

The resource potential hypothesis might also account for the stability of territory size during temporal increases in food abundance, as the reduction of territory size might result in territorial neighbours taking-over the abandoned locations: likely incurring high costs of reclaiming original territory borders by means of aggressive conflicts with an equipollent opponent, which likely makes this strategy less profitable then tolerance towards subordinates that can be more easily expelled (Parker, 1974) once changing food conditions demand so.

4. Conclusions

By reviewing empirical studies on territorial migratory songbirds I found sparse evidence for behavioural changes associated within the investigated components of territoriality (site fidelity, territory size and territorial aggression). Of all these components of territorial behaviour, the effect of food abundance on territory size was quantitively the best explored, though no effect was found in study systems where territories were already established. Site fidelity was found to be positively correlated with food abundance in one study, which was in contrast with the findings in another research. The single study on territorial aggression and further observations in other studies suggest that behavioural changes in territorial aggression are however occurring, and possible precede changes in spatial behaviour. However, as the limited studies were unevenly distributed over these behavioural components and did not simultaneously cover the influence of food abundance on changes within these behaviours, the existence of an overall hierarchy of flexibility in territorial behaviour remains unexplored.

I conclude that more studies on the influence of food conditions on territorial behaviours are highly necessary in order to understand the widespread phenomenon of non-breeding territoriality in songbirds. Preferably future studies illuminate the different components that constitute territorial behaviours in order to establish the existence of a hierarchy in behavioural mechanisms, and hence the overall flexibility that territorial migrant songbirds have at their disposal to cope with spatiotemporally shifting food conditions.

5. References

Beletsky, L.D. & Orians, G.H. 1989. Territoriality among male red-winged blackbirds. *Behav. Ecol. Sociobiol.* **24**: 333–339.

Brown, D.R. & Long, J.A. 2006. Experimental fruit removal does not affect territory structure of wintering Hermit Thrushes. *J. F. Ornithol.* **77**: 404–408.

Brown, D.R. & Sherry, T.W. 2008. Alternative strategies of space use and response to resource change in a wintering migrant songbird. *Behav. Ecol.* **19**: 1314–1325.

Cresswell, W. 2014. Migratory connectivity of Palaearctic-African migratory birds and their responses to environmental change: The serial residency hypothesis. *Ibis* **156**: 493–510.

Cuadrado, M. 1997. Why are migrant Robins (Erithacus rubecula) territorial in winter?: the importance of the anti-predatory behaviour. *Ethol. Ecol. Evol.* **9**: 77–88.

Davies, N.B. & Houston, A.I. 1981. Owners and satellites: the economics of territory defence in the Pied Wagtail, Motacilla alba. *J. Anim. Ecol.* **50**: 157–180. British Ecological Society.

Diggs, N.E., Marra, P.P. & Cooper, R.J. 2011. Resource limitation drives patterns of habitat occupancy during the nonbreeding season for an omnivorous songbird. *Condor* **113**: 646–654.

Drent, R.H. & Daan, S. 1980. The prudent parent: energetic adjustments in avian breeding. *Ardea* **55**: 225–252. Netherlands Ornithologists' Union.

Greenberg, R. 1995. Insectivorous migratory birds in tropical ecosystems: The breeding currency hypothesis. *J. Avian Biol.* **26**: 260.

Greenberg, R. & Salewski, V. 2005. Ecological correlates of wintering social systems in New World and Old World migratory passerines. In: *Birds of two worlds: the ecology and evolution of migration* (R. Greenberg & P. P. Marra, eds), pp. 336–358. Johns Hopkins University Press, Baltimore, Maryland.

Hixon, M.A. 1980. Food production and competitor density as the determinants of feeding territory size. *Am. Nat.* **115**: 510–530.

Järvistö, P.E., Calhim, S., Schuett, W., Sirkiä, P.M., Velmala, W. & Laaksonen, T. 2016. Carry-over effects of conditions at the wintering grounds on breeding plumage signals in a migratory bird: roles of phenotypic plasticity and selection. *J. Evol. Biol.* **29**: 1569–1584.

Levey, D.J. & Stiles, F.G. 1992. Evolutionary precursors of long-distance migration: resource availability and movement patterns in neotropical landbirds. *Am. Nat.* **140**: 447–476.

Marra, P.P. & Holmes, R.T. 2012. Consequences of Dominance-Mediated Habitat Segregation in American Redstarts during the Nonbreeding Season. *Auk* **118**: 92–104.

Moreau, R.E. 1972. *The Palearctic - African bird migration systems*. Academic Press, London.

Newton, I. 2008. *The migration ecology of birds*. Academic Press, Amsterdam.

Norris, D.R., Marra, P.P., Kyser, T.K., Sherry, T.W. & Ratcliffe, L.M. 2003. Tropical winter habitat limits reproductive success on the temperate breeding grounds in a migratory bird. **271**: 59–64.

Parker, G.A. 1974. Assessment strategy and the evolution of fighting behavoiur. *J. Theor. Biol.* **47**: 223–243.

Saino, N., Szép, T., Ambrosini, R., Romano, M. & Møller, A.P. 2004. Ecological conditions during winter affect sexual selection and breeding in a migratory bird. *Proc. R. Soc. B Biol. Sci.* **271**: 681–686.

Sherry, T., Johnson, M. & Strong, A. 2005. Does winter food limit populations of migratory birds? In: *Birds of two worlds: Advances in the ecology and evolution of temperate-tropical migration systems*, pp. 414–425. Johns Hopkins University Press, Baltimore, MD.

Sherry, T.W. & Holmes, R.T. 1996. Winter habitat quality, population limitation, and conservation of neotropical-nearctic migrant birds. *Ecology* **77**: 36–48.

Smith, J.A.M., Reitsma, L.R. & Marra, P.P. 2011. Influence of moisture and food supply on the movement dynamics of a nonbreeding migratory bird (Parkesia noveboracensis) in a seasonal landscape. *Auk* **128**: 43–52. Oxford University Press.

Stenger, J. 1958. Food habits and available food of Ovenbirds in relation to territory size. *Auk* **75**: 335–346. Oxford University Press.

Studds, C.E. & Marra, P.P. 2005. Nonbreeding habitat occupancy and population processes: an

upgrade experiment with a migratory bird. *Ecology* **86**: 2380–2385.
Tobias, J.O.E. 1997. Asymmetric territorial contests in the European robin. *Anim. Behav.* **54**: 9–21.
Tye, A. 1986. Economics of experimentally-induced territorial defence in a gregarious bird, the Fieldfare Turdus pilaris. *Ornis Scand.* **17**: 151–164.
Wilson, E.O. 1975. *Sociobiology: The new synthesis*. Harvard University Press, Harvard.