Reindeer carcasses provide foraging habitat for insectivorous birds of the alpine tundra

Rudy Badia[1], Sam MJG Steyaert[1, 2, 3*], Stefano Puliti[4], Rakel Blaalid[5] & Shane C. Frank[2]

[1] Faculty of Environmental Sciences and Natural Resource Management, Norwegian University of Life Sciences, NO-1432 Ås, Norway
[2] Faculty of Technology, Natural Sciences, and Maritime Sciences, Department of Natural Sciences and Environmental Health, University of South-East Norway, NO-3800 Bø i Telemark, Norway
[3] Faculty of Biosciences and Aquaculture, Nord University, NO-7713 Steinkjer, Norway
[4] Norwegian Institute of Bioeconomy Research, NO-1430 Ås, Norway
[5] Norwegian Institute for Nature Research, NO-5008 Bergen, Norway
* Correspondence: sam.steyaert@nord.no

Abstract. On August of 2016, almost an entire herd (n = 323) of wild tundra reindeer (*Rangifer tarandus*) was killed by lightning on Hardangervidda in southern Norway. While conducting fieldwork for another study in 2017, we opportunistically registered the occurrence and behaviour of birds on carcasses from this mass die-off. Several passerine species other than corvids were observed actively foraging on arthropods, such as blowfly (Calliphoridae sp.) adults and larvae, which are typically associated with carcass decomposition. We quantified observations of those birds, and described their foraging behaviour at the carcass site. In decreasing order of abundance, five passerine species were observed taking arthropods at the site: Meadow Pipit *Anthus pratensis*, Northern Wheatear *Oenanthe oenanthe*, Common Reed Bunting *Emberiza schoeniclus*, Bluethroat *Luscinia svecica*, and Lapland Bunting *Calcarius lapponicus*. Systematic surveys of passerines utilizing carcass sites would further our understanding of how such resources may affect behaviour and life history of various bird species.

Keywords: alpine tundra, carrion ecology, foraging ecology, passerines, *Rangifer tarandus*

INTRODUCTION

Carcasses of large terrestrial animals are ephemeral resource pulses that affect all trophic levels in the food chain, including soil microbiota, vegetation, invertebrates, and vertebrates (Barton et al. 2013, Benbow et al. 2019). Many effects emerge at the local scale (e.g. altered soil microbiota) (Crippen et al. 2015), whereas others may affect entire landscapes through nutrient redistribution by scavengers (Benbow et al. 2015, DeVault et al. 2003) or through directed endozoochory towards carcass sites. The latter implies that animals disperse plant seeds through ingestion (endozoochory) in disproportionate numbers towards microsites that are ideal for germination and establishment (Wenny & Levey 1998). Such directed endozoochory towards carcasses has been shown by Steyaert et al. (2018) with scavengers. Carcasses can eventually become biodiversity hotspots and facilitate interactions between species (Benbow et al. 2015, Martin 2016). For example, scavengers and invertebrates typically compete for carcass biomass (Beasley et al. 2015), whereas insect life at the carcasses facilitates high densities of insectivores (Moreno-Opo & Margalida 2013).

On 26 August 2016, nearly an entire herd (n = 323) of wild tundra reindeer (*Rangifer tarandus*) was killed by lightning north of lake Vesle Saure on Hardangervidda, Norway. All carcasses were left on-site (areal extent: ca 200 × 50m), with the exception of heads, which were removed by the authorities for the screening of Chronic Wasting Disease. We initiated a long-term research project, REINCAR, at the carcass concentration in Vesle Saure to assess how reindeer carcasses affect the alpine tundra ecosystem. This site provides a unique field laboratory for testing a multitude of ecological questions related to carrion ecology and alpine ecosystem processes.

During fieldwork for another study in August 2017 (Steyaert et al. 2018) , i.e. one year after the mass die-off, we made incidental observations of the foraging strategies of passerines (i.e., Meadow Pipit *Anthus pratensis*, Northern Wheatear *Oenanthe oenanthe*, Common Reed Bunting *Emberiza schoeniclus*, Bluethroat *Luscinia svecica*, and Lapland Bunting *Calcarius lapponicus*) feeding on insects associated with carcass decomposition (predominantly blowfly adults and their larvae Calliphoridae sp.) in and around the carcasses. Here, we describe our observations (including foraging behaviour) and discuss the potential ecological role of carrion for these passerine species.

METHODS

The carcass site is located 1220 m a.s.l within an alpine tundra ecosystem on the Hardangervidda plateau in Southern Norway (see Steyaert et al. 2018 for details). We opportunistically conducted surveys (n = 7, between 45 and 180 min each, totalling about 11 h) at the carcass site between 8 and 12 August 2017. Avian activity was observed but not quantified from 8–10 August, given the initial focus of the Steyaert et al. (2018) study, while the total and percentage of observations were calculated for the 11 and 12 August (Table 1). Those surveys (3 h each) were conducted in the early morning (06:00–09:00), whereas the others were conducted whenever time was available during daylight hours. In addition to 2017, observations were made from 3–5 August 2018 (two years after the carcass die-off). Bird foraging and behavioural observations were made using 10 × 42 binoculars. Given the tendency of birds to remain hidden (e.g. Lapland Bunting and Reed Bunting), we could not always identify the food items taken. Corvids were observed throughout the carcass decomposition process, when they were scavenging on carcass tissue.

For the purpose of this study, only behaviour of passerines foraging on arthropods (i.e., confirmed through direct observation or those likely foraging for arthropods based on bird biology) at the carcass site are presented. We used the foraging classification of Remsen & Robinson (1990) to describe the foraging behaviour of each bird species at the carcass site.

RESULTS

In total, 262 observations of individual passerines were registered, although double counts of individuals cannot be excluded. Foraging passerines, in addition to corvids, were observed throughout the day, with no apparent peak in activity detected. In order of decreasing abundance, the species observed foraging were Meadow Pipit, Northern Wheatear, Bluethroat, Common Reed Bunting, and Lapland Bunting (Table 1). The birds observed were taking mostly blowfly Calliphoridae sp. and crane fly Tipulidae sp. larvae and adults, as well as other unidentified arthropods. We did not quantify the abundance of the Ring Ouzel *Turdus orquatus*, though present at and around the site, as we were not able to discern whether or not they were foraging on arthropods.

Meadow Pipit. The Meadow Pipit was the most frequently observed bird (51.5% of all individuals) of the five species foraging on arthropods at the carcass site, with up to 80 individuals occurring at once and in close proximity to one another (< 1 m). The birds did not appear deterred by our presence and were frequently within very close range (3–5 m) of the field crew (n = 9). During 13 observations, Meadow Pipits at the site caught large adult Calliphoridae flies and larvae. We observed several feeding behaviours from the Meadow Pipit. They (1) leaped forward above the substrate surface taking insects, (2) entered the carcass cavity and performed the surface manoeuvre of reaching-up and reaching-out (rather than using flight) to get insects crawling on the inner wall of the carcasses, (3) lunged forward by darting or rushing (as opposed to leaping/jumping into the air) to capture prey, and (4) used their bills to probe the softer carcass tissue to dislodge larvae.

Northern Wheatear. This species was the second most frequently observed passerine species at the carcass site (24.8%) that foraged on arthropods. Up to 13 birds could be seen at a single time. We observed this ground-dwelling species walking or hopping in search of insects (Kaboli et al. 2007). Their predominant foraging manoeuvre was a 'peck', with several observations of birds pecking for larvae from the carcasses. Northern Wheatears were occasionally seen taking a few steps before aerial hawking (aerial foraging/attacking insects). Individuals were also detected performing an outward sally-strike by perching on the ground and quickly charging after flying insects. We were unable to identify the prey items taken by Northern Wheatears, but we presume that they foraged for Calliphoridae and Tipulidae larvae (Del Hoyo et al. 1992), considering their conspicuous occurrence and high abundance at the site. We only observed female or juvenile birds foraging at the site.

Bluethroat. In total, 13.3% of all individuals observed foraging were Bluethroats. Some individual Bluethroats chased one another, suggesting antagonistic behaviour among individuals. Bluethroats were skittish, flying from one perch to another presumably to avoid scuffles, and remained alert to their surroundings. We observed female and individuals with juvenile-type plumage surface-gleaning and manoeuvring after Diptera at the carcasses.

Common Reed Bunting. We detected up to four Reed Buntings (8.4% of all counted individuals) at the same time at the carcass site. None of the detected birds had the distinctive black hood typical of an adult male. Instead, all had the markings of either drab females or first-year type birds. The Reed Buntings remained in relatively close proximity to cover (e.g. vegetation with height of ~45cm and cover of ~50%). The birds were skulking (moving in a concealed manner) through the vegetation and around the carcasses. On several occasions, we observed them picking small flies and Calliphoridae larvae from carcasses. The birds were not observed taking the larger blowflies.

Lapland Bunting. Of the five passerine species foraging on arthropods at the site, the Lapland Bunting was the least detected species (1.9% of all individuals). We only observed single individuals, with birds hidden

Table 1. Observed bird species foraging on arthropods at a reindeer mass die-off site on Hardangervidda, Norway, in August 2017, one year after the die-off.

Species	Family	8 – 10 Aug	11 Aug	12 Aug	% total observed	Foraging manouver	Food item taken	Age/sex
Meadow Pipit *Anthus pratensis*	Motacillidae	Observed	80	55	51.5	walk/run lunged, leap forward probe	Calliphoridae Tipulidae	Juv., Ad.
Northern Wheatear *Oenanthe oenanthe*	Muscicapidae	Observed	25	40	24.8	walking/hopping pecking aerial hawking	Calliphoridae Tipulidae	Juv., F
Bluethroat *Luscinia svecica*	Muscicapidae	Observed	14	20	13.3	gleaning	Tipulidae	Juv, F
Common Reed Bunting *Emberiza schoeniclus*	Emberizidae	Observed	12	10	8.3	skulking	Small Diptera	Juv., F
Lapland Bunting *Calcarius lapponicus*	Calcariidae	NA	3	2	1.9	running picking gleaning	Small Diptera Calliphoridae larvae	Juv., F

among the short vegetation or between carcasses. The birds were skittish. They ran from one cover patch to the next, foraging in between by picking and gleaning at food items on the ground. We were unable to identify food items taken by the Lapland Bunting, but we presume they were foraging on arthropods.

During a revisit to the carcass site in August 2018, very few birds were detected foraging at the carcass site. We only observed three Meadow Pipits, four Northern Wheatears, and five Common Reed Buntings, and no Bluethroats or Lapland Buntings.

DISCUSSION

Our observations demonstrate that passerines of the alpine tundra exploit reindeer carcasses sites for insects. The fact that passerines forage on insects at animal carcasses is not a unique phenomenon, but only a few examples exist in literature. Moreno-Opo & Margalida (2013) have investigated carcass-use by feeding passerines. For that study, 18 species of passerines (6 corvids and 12 non-corvids) and several other species foraged on arthropods at supplementary feeding stations (using carrion) that targeted vultures. In the Pacific Northwest of North America, Winter Wrens *Troglodytes troglodytes* use salmon carcasses as foraging habitat for chironomid larvae during autumn and adult flies from overwintering eggs during the subsequent spring (Christie & Reimchen 2008). Socorro Thrashers *Mimodes graysoni* sometimes forage on blowflies from sheep (*Ovis* sp.) carcasses (Brattstrom & Howell 1956), and European Stonechat *Saxicola rubicola* use carcasses sites as foraging grounds in late summer and early spring (Gu et al. 2014). This indicates that large terrestrial animal carcasses may provide important food subsidies not only for scavengers (e.g. Common Raven *Corvus corax*), but also for omnivorous and insectivorous bird species, and they may facilitate coexistence among several taxa (Hågvar et al. 2009). In our study, avian activity appeared to have significantly decreased in 2018 compared to 2017, when the decomposition of the carcasses was at an earlier stage and with more available soft tissue for insect larvae. In 2018, the most common insect seemed to be small dipterids (Phoridae), which birds did not appear to forage on, probably due to their smaller size and presumably lower energy content in relation to the foraging costs in catching them. It should be noted that the summer of 2018 was very dry and warm, which could have influenced insect abundance. The effect of weather (e.g. hot, windy, overcast, or rain) on avian activity at the carcass site was not evident, as birds were observed foraging during variable weather conditions.

Lapland Bunting, Meadow Pipit, and Northern Wheatear have been shown to shift food selection to

take advantage of several available and abundant food sources in their breeding grounds (Hågvar et al. 2009), and Northern Wheatears supplement their diet with crowberry (Del Hoyo et al. 1992). The Meadow Pipit is known to forage on a wide range of insects <5mm long. The stomach content of early season hatchlings can contain up to 85% Tipulidae and Coleoptera, and drops to 41% on the second brood (Del Hoyo et al. 1992). Bluethroats at the study site took adult and larval flies of Tipulidae, Coleoptera, and Diptera, which is a feeding pattern that has been reported elsewhere (Del Hoyo et al. 1992). Guzy & McCaffery (2002) observed Bluethroats gleaning for insects from low vegetation and the ground, turning over leaves and soil, and hawking after flying insects. Lapland Bunting in the breeding season feed mainly on Diptera, especially on Tipulidae and opportunistically on blowfly larvae at carcasses (Del Hoyo et al. 1992). However, given that they feed on insects with a similar nutritional and niche overlap as other bird species at the study site, e.g. the Meadow Pipit, Northern Wheatear (as documented by Hågvar et al. 2009), it is likely that they fed on similar insects present in the carcass area. At the site, many adult blowflies had wrinkled wings, which indicates that they had only recently emerged from the pupal stage (Bhat et al. 2011). These insects were rather slow (e.g. we could easily grab the blowflies with our fingers) and were thus easy prey for the insectivorous and omnivorous birds present. Whereas blowflies are typically associated with carcasses, it remains unclear to what extent Tipulidae, a common food item in our observations, are associated with carcasses. We also observed an unusually large flock of Ring Ouzels (~60 individuals) about 700m from the carcass site. As an omnivorous species, the Ring Ouzel shifts its diet from invertebrates during the breeding period to fruits in the post-fledgling period (Del Hoyo et al. 1992), suggesting that they could have foraged on insects at the site prior to and after our fieldwork.

As much as 45% dietary overlap between Northern Wheatear and Meadow Pipit has been documented during summer (Hågvar et al. 2009), suggesting these birds may compete for resources. However, we did not observe antagonistic behaviour between individuals of these two species at the carcass site. We suggest that an overabundance of invertebrates may have facilitated both species to occur simultaneously at the carcass site. Hågvar et al. (2009) found that Northern Wheatears switched from a crowberry-dominated diet in August to a Lepidoptera larvae-based diet (70% of dry weight) in September. They found that the dietary overlap between the Meadow Pipit, Northern Wheatear, and Snow Bunting *Plectrophenax nivalis* was lowest during the early and late periods of the snow-free season and highest in July and August, when the production of invertebrates reaches its peak. Therefore, these birds appear to be very flexible in shifting their diets according to food item availability across the landscape (Hågvar et al. 2009).

At the site, a high prevalence of female and juvenile individuals was seen foraging for arthropods. Male individuals were not detected foraging at the site, with the reason for their absence unclear. Nevertheless, age-dependent skewed sex ratios have been documented at carcass sites before, for example, with Andean condor *Vultur gryphus* males outnumbering females as much as 4x (Lambertucci et al. 2012). Such sex biases in habitat use can affect life history. For example, it has been documented that individual American Redstarts (*Setophaga ruticilla*) in a primarily female-biased habitat experienced a degraded physiological condition affecting migration departure, migration pattern, and arrival at the breeding grounds (Marra & Holberton 1998).

It remains unknown whether this community assemblage of birds at the carcass site represents resource partitioning or an artefact of opportunistic data collection. Our observations could be biased by an ‚observer effect', in which shy birds are under-represented and less shy birds might be over-represented, in terms of both presence and abundance. Using camera traps or other remote monitoring methods would reduce such observer effects. Although an experimental design is required to go beyond speculation, our study provides direction for future research on how mass die-offs can affect foraging ecology of birds, and therefore fitness and potentially population dynamics.

Ungulate mass die-offs and carcasses in general are resource pulses that could help explain fluctuations in passerine populations and their life history (Gende & Willson 2001). Such mass inputs of nutrients made available to birds across the landscape might be more important than previously considered. A better understanding of how carcass biomass is used by species and how it can alter habitat could help direct conservation efforts for scavengers or for species that indirectly benefit from carcasses. For example, obligate scavengers like vultures play a vital role in the redistribution of nutrients derived from carcasses (Beasley et al. 2015). Furthermore, facultative scavengers can direct plant seed to carcass locations and potentially contribute to genetic diversity of plant populations (Steyaert et al. 2018). Science-based arguments can then lead to more scavenger-tolerant and -benefiting legislation and regulation (Margalida et al. 2012).

Mass die-offs of large ungulates are considered to be rare events, with the exception, however, of wildebeest *Connochaetes taurinus*, where many migratory animals drown annually in their attempt to cross the Mara river, in Kenya. The consequences are altered river ecosystems affecting nutrient cycling and food webs (Subalusky et al. 2017). Mass die-offs of reindeer

and other ungulates in the alpine tundra may be much more common than previously expected, e.g., due to avalanches during the winter. Such events, however, often remain unreported in the scientific literature (Andersen et al. 2007). It remains uncertain to what degree such a protein rich resource in the environment could benefit Scandinavian high-altitude birds. Given the observational nature of this study, we suggest more systematic surveys of avian insectivorous foraging at carcass sites, across a range of biomass amount from single carcasses to the level of mass die-offs. Such surveys could reveal potentially important impacts of carcasses on life history and population dynamics of various bird species.

REFERENCES

Andersen, R., Jordhøy, P. & Strand, O. 2007. Svarthøskredet i Snøhetta; håntering og prøvetaking av dyrene. Villreinen 21: 74–79.

Barton, P.S., Cunningham, S.A., Lindenmayer, D.B. & Manning, A.D. 2013. The role of carrion in maintaining biodiversity and ecological processes in terrestrial ecosystems. Oecologia 171: 761–772.

Beasley, J.C., Olson, Z.H. & DeVault, T.L. 2015. Ecological role of vertebrate scavengers. In: B. E.M., T. J.K. & A.M. Tarone (Eds.), Carrion Ecology, Evolution, and Their Applications (pp. 107–129): CRS Press.

Benbow, M.E., Barton, P.S., Ulyshen, M.D., Beasley, J.C., DeVault, T.L., Strickland, M.S., Tomberlin, J.K., Jordan, H.R. & Pechal, J.L. 2019. Necrobiome framework for bridging decomposition ecology of autotrophically and heterotrophically derived organic matter. Ecological Monographs 89: 1–19.

Benbow, M.E., Tomberlin, J.K. & Tarone, A.M. (Eds.). 2015. Carrion Ecology, Evolution, and Their Applications: CRC press. pp. 577.

Bhat, M.A., Shrivastav, A.B., Qureshi, S.R. & Quadri, S.A. 2011. Forensic exploitation of veterinary entomology. International Journal for Agro Veterinary and Medical Sciences 5: 429–437.

Brattstrom, B.H. & Howell, T.R. 1956. The birds of the Revilla Gigedo islands, México. The Condor 58: 107–120.

Christie, K.S. & Reimchen, T.E. 2008. Presence of salmon increases passerine density on Pacific Northwest streams. The Auk 125: 51–59.

Crippen, T.L., Benbow, E.M. & Pechal, J.L. 2015. Microbial interactions during carrion decomposition. In: E.M. Benbow, J.K. Tomberlin & A.M. Tarone (Eds.), Carrion ecology, evolution, and their applications (pp. 31-52): CRC press.

Del Hoyo, J., Elliott, A. & Sargatal, J. 1992. Handbook of the birds of the world (Vol. 1): Lynx edicions Barcelona.

DeVault, T.L., Rhodes, J.O.E. & Shivik, J.A. 2003. Scavenging by vertebrates: behavioral, ecological, and evolutionary perspectives on an important energy transfer pathway in terrestrial ecosystems. Oikos, 102: 225–234.

Gende, S.M. & Willson, M.F. 2001. Passerine densities in riparian forests of southeast Alaska: potential effects of anadromous spawning salmon. The Condor 103: 624–629.

Gu, X., Haelewaters, D., Krawczynski, R., Vanpoucke, S., Wagner, H.-G. & Wiegleb, G. 2014. Carcass ecology– more than just beetles. Entomologische Berichten, 74: 68–74.

Guzy, M.J. & McCaffery, B.J. 2002. Bluethroat: Luscinia Svecica. Birds of North America.

Hågvar, S., Glesne, O. & Østbye, E. 2009. Food habits and niche overlap in three alpine passerine birds, South Norway. Ornis Norvegica 32: 56–73.

Kaboli, M., Aliabadian, M., Guillaumet, A., Roselaar, C.S. & Prodon, R. 2007. Ecomorphology of the wheatears (genus Oenanthe). Ibis 149: 792–805.

Lambertucci, S.A., Carrete, M., Donázar, J.A. & Hiraldo, F. 2012. Large-scale age-dependent skewed sex ratio in a sexually dimorphic avian scavenger. PloS one 7(9), e46347.

Margalida, A., Carrete, M., Sánchez-Zapata, J.A. & Donázar, J.A. 2012. Good news for European vultures. Science 335(6066): 284–284.

Marra, P.P. & Holberton, R.L. 1998. Corticosterone levels as indicators of habitat quality: effects of habitat segregation in a migratory bird during the non-breeding season. Oecologia, 116: 284–292.

Martin, C. 2016. From death comes life. Current Biology 26: 548–552.

Moreno-Opo, R. & Margalida, A. 2013. Carcasses provide resources not exclusively to scavengers: patterns of carrion exploitation by passerine birds. Ecosphere 4: 1–15.

Remsen, J.J. & Robinson, S.K. 1990. A classification scheme for foraging behavior of birds in terrestrial habitats. Studies in Avian Biology 13: 144–160.

Steyaert, S.M.J.G., Frank, S., Puliti, S., Badia, R., Arnberg, M., Beardsley, J., Økelsrud, A. & Blaalid, R. 2018. Special delivery: scavengers direct seed dispersal towards ungulate carcasses. Biology letters 14(8).

Subalusky, A.L., Dutton, C.L., Rosi, E.J. & Post, D.M. 2017. Annual mass drownings of the Serengeti wildebeest migration influence nutrient cycling and storage in the Mara River. Proceedings of the National Academy of Sciences 114: 7647–7652.

Wenny, D.G. & Levey, D.J. 1998. Directed seed dispersal by bellbirds in a tropical cloud forest. Proceedings of the National Academy of Sciences 95: 6204–6207.