

Co-evolution of jaegers (*Stercorarius* spp.) and arctic lemmings (*Dicrostonyx* spp. and *Lemmus* spp.) and the formation of the jaeger guild: an hypothesis

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ABSTRACT

Background: The Fennoscandian tundra differs from other arctic regions hosting brown lemmings (*Lemmus* spp.) in that it supports exceptionally low numbers of avian predators. Jaegers (*Stercorarius* spp.) play a central role in the guild of predators exploiting lemming outbreaks, as they are long-lived and have a vast supply of marine survival resources. Collared lemmings (*Dicrostonyx* spp.) evolved much earlier than brown lemmings (*Lemmus* spp.),

Hypothesis: Lemming–vegetation dynamics and summer predation are causally interconnected. Avian predators that are adapted to exploit lemming outbreaks evolved in tundra areas where lemming–vegetation interactions generate density oscillations with a mean period short enough to provide dependable breeding resources for predators.

Predictions: Long-tailed jaegers (*Stercorarius longicaudus*), primarily exploiting collared lemmings, diverged from parasitic jaegers (*S. parasiticus*) more than 2 million years ago. Pomarine jaegers (*S. pomarinus*) evolved more recently in response to the emergence of regular oscillations of brown lemming populations. The current breeding distribution of jaegers should reflect the distribution of the two lemming genera, except for areas where the oscillations generated by lemming–plant interactions are too erratic to provide dependable breeding resources.

Empirical evidence: Our hypothesis accounts for the current distributions, behaviours, and ecologies of the three jaeger species. In addition, long-tailed jaegers did diverge early from other Stercorariidae. But we still do not know whether the timing of the divergence matches the evolution of collared lemmings. Evidence suggests that either: (1) Pomarine jaegers diverged from the skua (*Catharacta* spp.) lineage early, before skuas had developed their distinctive morphological traits; or (2) Pomarine jaegers diverged recently from great skuas (*Catharacta skua*) and then reverted to the ancestral jaeger morphology. Only the latter interpretation is consistent with our hypothesis, so we need to have more reliable timing of the evolution of long-tailed and Pomarine jaegers.

Keywords: Arctic, lemming–vegetation dynamics, predation, predator–prey co-evolution, tundra.

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INTRODUCTION

Co-evolution is defined as reciprocal adaptation of two or more species in response to one another (Futuyma and Slatkin, 1983). Although numerous examples exist of the evolutionary response of prey to their enemies (for a review, see Vamosi, 2005), less is known about the role of prey adaptation in the divergence and diversification of predators (e.g. Brodie and Brodie, 1999; Dietl, 2003). In the Arctic, which is characterized by simple predator–prey communities and where vertebrate prey populations, such as lemmings, often undergo oscillating dynamics with long periods of low densities, predators have evolved species-specific adaptations to exploit rodent peaks for maximizing their fitness. Due to regional variations in landscape composition across the arctic tundra, processes governing plant–lemming–predator interactions have generated varying ecologies, behaviours, and breeding distributions of predator species. Deciphering evolutionary interactions between arctic predators and their lemming prey can help us better understand the regional patterns of summer predation pressure, especially why some arctic lemming populations are heavily ‘cropped’ by predators in outbreak summers (Pitelka, 1973; Batzli *et al.*, 1980; Gilg *et al.*, 2006; Therrien *et al.*, 2014), whereas others are not (Krebs, 1964; Oksanen and Oksanen, 1992; Framstad *et al.*, 1993; Hoset *et al.*, 2014; L. Ruffino, unpublished).

Our point of departure is the simulation study of Oksanen *et al.* (2013), which explored the impacts of different levels of summer predation on density oscillations, generated by lemming–plant interactions. In their simulations, summer predation pressure was varied independently of the characteristics of lemming–vegetation dynamics. In the empirical section, Oksanen *et al.* (2013) noted that in nature summer predation pressure varies geographically. Compared with other parts of the circumpolar tundra, the Fennoscandian tundra is characterized by low numbers of avian predators and, especially, by the absence of Pomarine jaegers [*Stercorarius pomarinus* (see Chernyavski and Tkachev, 1982; Wiklund *et al.*, 1999)]. The contrast was pointed out as early as 1992 by Frank Pitelka (personal communication), but no explanation has been provided to date.

In an attempt to explain the regional differences in the size of the predator pool, we hypothesize that lemming–vegetation dynamics and summer predation are causally interconnected. Applying the principle that evolutionary events are triggered by ecological opportunities (e.g. Losos, 2010), we propose that in those tundra areas where lemming–plant interactions generate lemming outbreaks predictably and at time intervals no longer than 6 years, predators specializing on lemmings as breeding resources will evolve. In this paper, we focus on the jaeger guild (*Stercorarius* spp.) because of its circumpolar summer distribution and the varying ecologies, behaviours, and breeding strategies of its member species. Jaegers are long-lived birds and utilize pelagic resources during the non-breeding season (Furness, 1987), which allow them to persist in high numbers despite infrequent breeding opportunities. Moreover, the behavioural and morphological traits involved in their kleptoparasitic foraging strategy, such as agility, aggressiveness, and elongated tail feathers that act as rudders, are also advantageous for the exploitation of lemmings.

The jaeger guild consists of three species. The parasitic jaeger (*S. parasiticus*) preys opportunistically on lemmings, but also requires a reasonably steady food supply, principally in the form of marine-based resources, to breed successfully (Andersson and Götmark, 1980; L. Ruffino, unpublished). The long-tailed jaeger (*S. longicaudus*) is smaller and can supplement its summer diet with invertebrates and berries, but successful breeding depends to a large extent on small rodents, usually collared lemmings [*Dicrostonyx* spp.

(Andersson, 1976; Pattie, 1977; de Korte and Wattel, 1988; Gilg *et al.*, 2006; Meltofte and Høye, 2007)]. The Pomarine jaeger (*S. pomarinus*) is the largest species and depends on high brown lemming (*Lemmus* spp.) densities for breeding (Maher, 1970, 1974). All three jaeger species are pelagic kleptoparasites during the non-breeding season (Furness, 1987).

The two genera of arctic lemmings, i.e. collared lemmings (*Dicrostonyx* spp.) and brown lemmings (*Lemmus* spp.), have evolved independently (Fig. 1a). Collared lemmings utilize dicotyledonous plants and therefore prevail in heath-type tundra habitat (Batzli, 1993; Morris *et al.*, 2000), which also exists in the High Arctic (Fuller *et al.*, 1977; Jarrell and Fredga, 1993; Gilg *et al.*, 2006). Brown lemmings exploit mosses and graminoids and are therefore most abundant on moist lowland tundra in low and middle arctic areas (Batzli *et al.*, 1980; Batzli, 1993; Jarrell and Fredga, 1993). Collared lemmings evolved on the tundra at the dawn of the Pleistocene, about 2.6 million years ago, whereas truly tundra-adapted brown lemmings diverged from wood lemmings (*Myopus* spp.) later, probably only 400,000–500,000 years ago (Fejfar, 1965; Guthrie and Matthews, 1971; Jarrell and Fredga, 1993; Galewski *et al.*, 2006; Robovský *et al.*, 2008; see also Batzli, 1993; Stenseth and Ims, 1993).

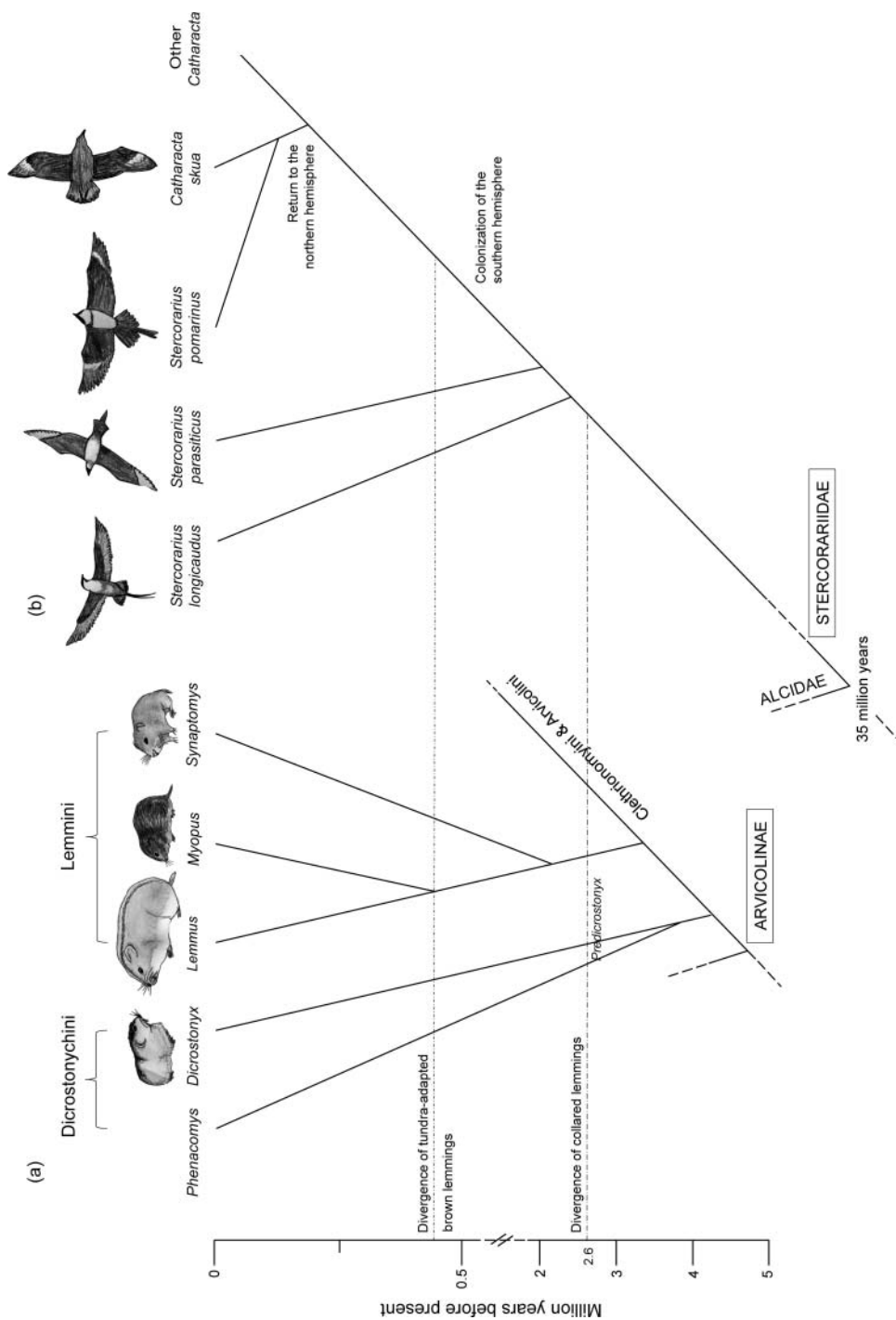
We hypothesize that long-tailed and Pomarine jaegers co-evolved with collared and brown lemmings, respectively. If so, these two jaeger species evolved at different times and the evolution of the Pomarine jaegers occurred more recently in response to the comparatively recent evolution of brown lemmings. Our hypothesis also implies that the current breeding distribution of jaegers should reflect the distributions of the two lemming genera, except for areas where the oscillations generated by lemming–plant interactions are too erratic to provide dependable breeding resources.

METHODS

We tested our hypothesis by reviewing the evolutionary history of jaegers and the closely related skuas (*Catharacta* spp.), whose evolution is tightly intertwined with jaeger evolution. We also assessed the current breeding distributions, ecologies, and behaviours of jaegers and skuas to determine whether they are consistent with our hypothesis.

COMPARING OUR HYPOTHESIS TO EVOLUTIONARY FACTS

The first species belonging to the jaeger/skua clade (Stercorariidae) evolved in the Eocene, about 35 million years ago (Baker *et al.*, 2007; Mayr, 2011; Weir and Mursleen, 2012), when a warm climate prevailed even at high latitudes, whereas the evolution of arvicoline rodents began in the early Pliocene, about 5 million years ago (Galewski *et al.*, 2006; Robovský *et al.*, 2008) (Fig. 1a). During their long evolutionary history, the ancestors of jaegers and skuas remarkably converged with birds of prey. They became efficient hunters, sometimes taking even relatively large vertebrate prey (Andersson, 1999) in spite of the constraints imposed by their evolution from gull-like ancestors (Mayr, 2011; Weir and Mursleen, 2012). There is a consensus that the ancestral members of Stercorariidae resembled jaegers rather than skuas (Cohen *et al.*, 1997; Braun and Brumfield, 1998; Andersson, 1999; Ritz *et al.*, 2008; Chu *et al.*, 2009), i.e. they were relatively small and agile and had clearly different adult and juvenile plumages. De Korte and Wattel (1988) regard it as plausible that these basal skuas/jaegers were kleptoparasites and resembled modern parasitic jaegers (*S. parasiticus*) in morphology and lifestyle. As the parasitic jaeger is the only jaeger species able to breed without a reliance on terrestrial resources (Maher, 1961; Furness, 1987), its strategy does not depend on the existence of oscillating rodent populations.



We do not know when parasitic jaegers and the smallest jaeger species, the long-tailed jaeger, diverged. We know only that it happened well before the evolution of skuas (Cohen *et al.*, 1997; Chu *et al.*, 2009) (Fig. 1b). Thus synchrony between this divergence and the evolution of collared lemmings remains uncertain. But the available information is at least consistent with the prediction of our hypothesis and the suggestion of Maher (1974) and de Korte and Wattel (1988) that long-tailed jaegers evolved during the Pleistocene in ice-free high arctic refugia, which already supported collared lemmings but harboured few competing predators. Since ancestral collared lemmings (*Predicrostonyx*) were relatively small, like their modern relatives (*Dicrostonyx* spp.; body mass about 40 g), their exploitation selected for smaller body size (see also de Korte and Wattel, 1988) and increased agility in jaegers. On the other hand, reduced body size resulted in aggressive inferiority, as seen even today (e.g. Maher, 1974). It is thus likely that the ancestors of long-tailed jaegers started to rely on collared lemmings as breeding resources resulting in disruptive selection pressures and competitive speciation (Rosenzweig, 1978). Resource-rich coastal habitats were left for parasitic jaegers, which could also opportunistically exploit collared lemmings but did not depend on them.

The next profound evolutionary process in Stercorariidae was the evolution of skuas (*Catharacta* spp.) and Pomarine jaegers. This process remains enigmatic, but apparently took place less than 250,000 years ago (e.g. Cohen *et al.*, 1997; Ritz *et al.*, 2008; Chu *et al.*, 2009). Despite the current consensus that Pomarine jaegers are more closely related to skuas than to other jaegers, there are two contrasting interpretations of this evolutionary process; both views are supported by different kinds of empirical evidence. On the basis of nuclear DNA and skeletal morphology, Braun and Brumfield (1998) and Chu *et al.* (2009) proposed that skuas evolved in the northern hemisphere and that Pomarine jaegers diverged from that lineage at an early stage, retaining the ancestral jaeger traits (i.e. a clear difference between a juvenile gull plumage and a black-and-white adult plumage; elongated tail feathers; and small body size).

According to the other interpretation, advocated by Cohen *et al.* (1997) on the basis of mitochondrial DNA and ectoparasites (see also Ritz *et al.*, 2008), and proposed earlier by Andersson (1973) on the basis of behavioural traits, Pomarine jaegers are closely related to great skuas (*Catharacta skua*) and evolved relatively recently. According to the latter interpretation, skuas evolved in the southern hemisphere, presumably around 210,000 years ago, as proposed by Ritz *et al.* (2008; see also Fisher and Lockley, 1954; Furness, 1987; Andersson, 1999). It is plausible that the mobile ancestral parasitic jaegers found breeding opportunities on some sub-antarctic islands with high densities of breeding seabirds, which triggered their evolution towards a more predatory lifestyle (Ritz *et al.*, 2008). The persistently dark, juvenile-like plumage of skuas, which possibly evolved via neoteny (Andersson, 1999), and their large body size could have evolved as adaptations to a predatory life among dark cliffs and on a stormy

Fig. 1. Evolutionary histories of (a) the members of the Dicrostonychini and Lemmini tribes of arvicoline rodents (Arvicolinae), and (b) the members of Stercorariidae (jaegers, *Stercorarius* spp., and skuas, *Catharacta* spp.). The evolutionary history of rodents was reconstructed based on the previous work of Robovský *et al.* (2008) and of Koenigswald and Martin (1984; see also Stenseth and Ims, 1993); the evolutionary history of jaegers and skuas was reconstructed based on the molecular evidence provided by the work of Cohen *et al.* (1997) and Ritz *et al.* (2008). The timings in the jaeger/skua tree reflect our hypothesis of lemming/jaeger co-evolution and is only partially corroborated.

sea, where a dark bird is hard to detect (Furness, 1987; see also Andersson, 1973, 1976). Later, the ancestors of the great skua may have responded to similar opportunities on the high latitude islands of the northern hemisphere (Furness, 1987), and this would have provided the point of departure for the evolution of Pomarine jaegers (Cohen *et al.*, 1997).

As they evolved a predatory lifestyle, some ancestral great skuas may have started to utilize brown lemmings as breeding resources (see also Maher, 1970). In this new niche, natural selection would have favoured reversal of neoteny and a return to the ancestral jaeger morphology (for this and other scenarios, see Andersson, 1999). These skuas, which were evolving to become Pomarine jaegers, were then likely to exclude the smaller jaegers from the most resource-rich habitats (for a corresponding modern example, see Dawson *et al.*, 2011). Adaptation to the exploitation of brown lemmings was completed by the unique hunting behaviour of Pomarine jaegers, which are able to dig brown lemmings out from their burrows in flat and marshy tundra areas where lemmings nest close to the surface (Maher, 1970; Andersson, 1973).

Of the two contesting scenarios, only the latter is consistent with our hypothesis. The former is doubtless more parsimonious because the latter requires that the ancestors of Pomarine jaegers had crossed the equator and reversed their plumage pattern twice. However, many jaeger and skua species frequently cross the equator even today (Furness, 1987) and corresponding plumage changes occur frequently in larids (Crochet *et al.*, 2000). Moreover, the latter interpretation (Fig. 1b) connects the postulated evolutionary processes in Stercorariidae to new (brown lemmings, Fig. 1a) or unexploited (subantarctic island birds) ecological opportunities (see Losos, 2010), whereas the former scenario does not provide clear links between ecology and evolution.

STRUCTURE OF THE CONTEMPORARY JAEGER GUILD

In spite of the remaining uncertainties, our hypothesis (Fig. 1) smoothly links the past to the present. During the breeding season, parasitic jaegers prey opportunistically on rodents, but due to the combination of high breeding site fidelity and a strategy where reproduction is attempted regardless of rodent densities, parasitic jaegers require a reasonably steady food supply to breed [e.g. marine resources, birds (e.g. Andersson and Götmark, 1980; Furness, 1987)]. Their breeding distribution is circumpolar, including both subarctic and boreal coasts. Parasitic jaegers breed in varying densities, but because they are often ignored or barely considered in studies on lemming predators (e.g. Gilg *et al.*, 2006; Legagneux *et al.*, 2012; Therrien *et al.*, 2014), and as they seldom breed outside the vicinity of the coast, their impact on arctic lemmings at a regional scale has been regarded as minimal. Parasitic jaegers have thus been associated with the productive northern seas rather than with oscillating lemming populations.

The breeding distribution of long-tailed jaegers is circumpolar, with the exception of Iceland where they are missing, as are all arvicoline rodents. The species is common in the high arctic tundra regions where brown lemmings are absent (Pattie, 1977; Gilg *et al.*, 2006; Meltofte and Høye, 2007) and in dry inland tundra areas where habitat conditions favour collared lemmings (Maher, 1974). Long-tailed jaegers are aggressively inferior to Pomarine and parasitic jaegers but can supplement their summer diet with invertebrates and berries (Andersson, 1976; Pattie, 1977; de Korte and Wattel, 1988; Gilg *et al.*, 2006); successful breeding of long-tailed jaegers depends largely on small rodents. For example, at Alert, Ellesmere Island, Nunavut, Canada, *Dicrostonyx groenlandicus* represents 42% of the assimilated diet of adult long-

tailed jaegers in summer (Julien *et al.*, 2014). Breeding densities can reach up to 1 pair/km² in Nunavut (Julien *et al.*, 2014; Therrien *et al.*, 2014) and Greenland (Gilg *et al.*, 2006). Together with snowy owls and arctic foxes, long-tailed jaegers generate the summer declines typical for peak years of collared lemming oscillations (Gilg *et al.*, 2006).

The current breeding range of Pomarine jaegers extends from Pomor, European Russia, to Baffin Island, Canada, embracing all areas with extensive graminoid-rich lowland tundra, supporting brown lemming populations with fairly regular density oscillations (average period: 3–6 years). In summers with high brown lemming densities, the breeding density of Pomarine jaegers reaches up to 5 pairs/km² on Taimyr, Russia (van Kleef *et al.*, 2009), and up to 7.9 pairs/km² at Barrow, northern Alaska (Maher, 1970; Custer and Pitelka, 1987). Pomarine jaegers are dominant in aggressive encounters and can thus exclude other jaegers from graminoid-rich tundra habitats (Maher, 1974). Due to their high local densities, their predatory impact can be locally very high in these regions.

On the basis of the information summarized above, we propose that the interaction between evolution and ecology has created a jaeger guild structured by centrifugal community organization (Rosenzweig and Abramsky, 1986). In Fig. 2, we summarize our hypothesis concerning the breeding season niches of the three jaegers in areas where terrestrial resources other than rodents (invertebrates, berries, terrestrial birds) are not abundant enough to support breeding populations of any jaeger species. This applies to most arctic habitats but not to the most water-rich wetlands. The fundamental niches of each jaeger are delimited by their zero-isoclines in the rodent–marine resource phase plane, which we inferred from searching the literature for situations where aggressively superior competitors happened to be absent. The normally realized niches are those parts of the fundamental niche that do not overlap the fundamental niche of an aggressively superior competitor. The dependence of Pomarine jaegers on rodents as breeding resources implies that their isocline is a straight line, perpendicular to the rodent axis. By and large the same holds for long-tailed jaegers, as even individuals breeding close to the coast utilize little if any marine-based resources during the breeding season (L. Ruffino, unpublished data). However, in some high arctic areas with few or no parasitic jaegers, long-tailed jaegers can change strategy and start to breed using marine-based resources (Kampp, 1982; de Korte and Wattel, 1988). Their isocline thus bends leftwards and meets the marine resource axis. The ability of parasitic jaegers to supplement their diets with rodents implies that their isocline has a negative slope. But since they breed only in areas where they also have a reasonable chance to reproduce in rodent crash years, parasitic jaegers can choose only breeding sites which provide some marine-based resources, too. Their isocline must therefore have a horizontal asymptote in the phase plane of Fig. 2.

Our niche hypothesis (Fig. 2) thus implies that, without competition, all three species would be likely to choose to breed on coastal tundra, optimal for all because of the combination of periodically high lemming densities and access to marine resources. Yet, due to interspecific interactions, the smaller species usually have to settle in the less resource-rich habitats (Fig. 2). Due to their high breeding site fidelity (Barraquand *et al.*, 2014), the smaller species would probably show long response times if new breeding opportunities happened to emerge due to declines in their larger competitors. Hence, the ghost of competition past (Rosenzweig, 1991; Morris *et al.*, 2000) can be long-lived in the jaeger guild, and documenting active interspecific competition is difficult except in cases where breeding territories of different jaegers are adjacent to each other (Pitelka, 1973; Maher, 1974).

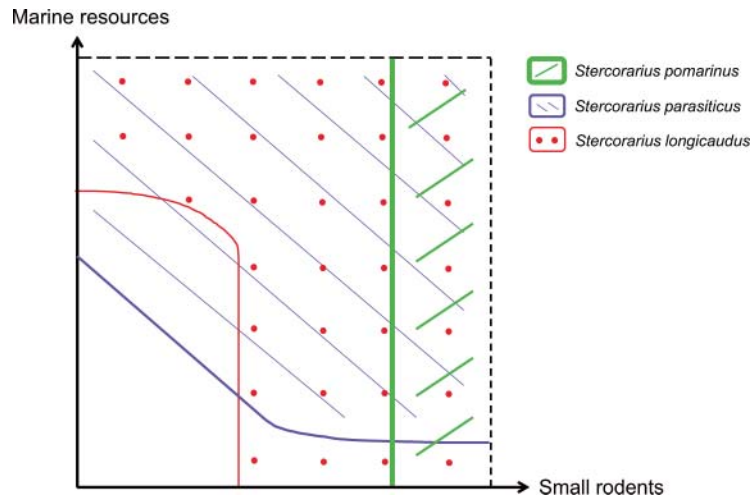


Fig. 2. Niche organization of the three jaeger species during the breeding season, expressed as zero isoclines (solid lines, representing the borders of fundamental niches) in the phase plane with densities of rodents and marine-based resources as axes. The thicknesses of the lines represent the aggressive rank orders of the species. The aggressively superior Pomarine jaegers depend on high rodent densities (in practice: brown lemmings, *Lemmus* spp.). Parasitic jaegers, next in the aggressive rank order, can opportunistically prey on rodents while utilizing marine resources. The long-tailed jaeger breeds in association with small rodents, but breeding on dependable marine resources is also possible. No species succeeds near the origin of the graph, where neither rodents nor marine resources are abundant.

FENNOSCANDIA: THE EXCEPTION THAT CONFIRMS THE RULE

One of our starting points was the observation that, unlike all other regions harbouring brown lemmings (*Lemmus* spp.), the Fennoscandian tundra does not support breeding populations of Pomarine jaegers, although they migrate in large numbers along Norwegian coasts (www.artsdatabanken.no) and occasionally breed in northernmost Norway (Øien, 2011). On the other hand, all long-term demographic records of Norwegian lemmings (*Lemmus lemmus*) reveal erratic dynamics, where lemmings can hover at low densities for periods of 10–20 years (Turchin *et al.*, 2000; Kausrud *et al.*, 2008; Kataev and Okulova, 2010; Olofsson *et al.*, 2014). A likely reason is a shortage of graminoid-rich habitats (Oksanen and Virtanen, 1995), which would buffer lemmings against catastrophic crashes (Oksanen *et al.*, 2013). Norwegian lemmings thus do not constitute dependable breeding resources and lack ecological opportunities for predators that depend on them.

Long-tailed jaegers, on the other hand, regularly breed in northern Fennoscandian tundra. Even though collared lemmings are absent from this region, the same niche has been taken over by grey-sided voles (*Myodes rufocanus*), which are of similar size and have regular 4–5 year cycles (Ekerholm *et al.*, 2001; see also Ims *et al.*, 2011; Hoset *et al.*, 2014). In lemming outbreak summers, Fennoscandian long-tailed jaegers exploit Norwegian lemmings too, but available lemming records show that even in northern inland areas where jaeger densities are highest (www.artsdatabanken.no; Andersson, 1976), long-tailed jaegers are not numerous enough to prevent positive summer population growth of Norwegian lemmings (Turchin *et al.*, 2000; Ekerholm *et al.*, 2001; Ims *et al.*, 2011; Olofsson *et al.*, 2014; L. Ruffino, unpublished). On the mountains of

southern Norway, where the regularly cyclic grey-sided voles are replaced by root voles (*Microtus oeconomus*), with basically lemming-like numerical dynamics [sudden outbreaks, separated by long periods of low numbers (Framstad *et al.*, 1993; see also Andreassen *et al.*, 2013)], long-tailed jaegers breed only sporadically [e.g. in the surroundings of water-rich wetlands on elevated inland plateaus (Falkenberg *et al.*, 2004; see also www.artsdatabanken.no)]. The southern breeding range limit of Fennoscandian long-tailed jaegers thus indicates its dependence on tundra areas with regularly oscillating populations of medium-sized arvicoline rodents, and also shows how range limits can act as pilot tests of ecological and evolutionary hypotheses (see Holt and Barfield, 2011).

CONCLUSIONS

We started from the assumption that the evolution of jaegers can be seen as a consequence of oscillatory dynamics of small rodent populations, emerging from the adaptation of rodents to arctic ecosystems. We found that this point of departure appears helpful in deciphering the seemingly contrasting results obtained in studies of arctic food web dynamics. The interplay between evolutionary and ecological dynamics discussed above appears to have generated geographical heterogeneity in predator–lemming–vegetation dynamics within different parts of the circumpolar tundra. While in some arctic areas the strong interaction is between lemmings and marine-subsidized predators (e.g. Legagneux *et al.*, 2012), in others, the strong interaction is between lemmings and plants, and summer predation is either negligible (Oksanen *et al.*, 2013; Olofsson *et al.*, 2014; L. Ruffino, unpublished) or periodically intense but nevertheless insufficient to prevent lemmings from depleting available winter forage plants (Batzli *et al.*, 1980).

By integrating our scenario of predator evolution with the population dynamical simulations of Oksanen *et al.* (2013), we conclude that out of the four possibilities considered by them, only two outcomes are evolutionarily plausible. The first case consists of systems where annually renewable resources are in short supply and lemming–vegetation interactions therefore generate extremely violent oscillations with long periods of very low lemming densities; such systems are unsuitable for predators (see Abrams and Roth, 1994). The other possibility pertains to cases where annually renewable forage plants abound and lemming–vegetation interactions therefore generate relatively regular lemming cycles. In such systems, the lemming peaks provide predators with dependable breeding resources, promoting the evolution and persistence of predators adapted to exploit lemming peaks. Consequently, the predatory impact has the potential to further reduce the amplitude of the lemming cycles and increase their regularity, which may (but need not) result in complete control of lemmings by predators. Understanding the dynamics of arctic food webs thus requires long-term experimental studies of all trophic levels in different parts of the circumpolar tundra.

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