BioOne COMPLETE

Effects of small mammal cycles on productivity of boreal ducks

Authors: Brook, Rodney W., Duncan, David C., Hines, James E., Carrière, Suzanne, and Clark, Robert G.

Source: Wildlife Biology, 11(1) : 3-11

Published By: Nordic Board for Wildlife Research

URL: https://doi.org/10.2981/0909-6396(2005)11[3:EOSMCO]2.0.CO;2

BioOne Complete (complete.BioOne.org) is a full-text database of 200 subscribed and open-access titles in the biological, ecological, and environmental sciences published by nonprofit societies, associations, museums, institutions, and presses.

Your use of this PDF, the BioOne Complete website, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at www.bioone.org/terms-of-use.

Usage of BioOne Complete content is strictly limited to personal, educational, and non - commercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

BioOne sees sustainable scholarly publishing as an inherently collaborative enterprise connecting authors, nonprofit publishers, academic institutions, research libraries, and research funders in the common goal of maximizing access to critical research.

Downloaded From: https://complete.bioone.org/journals/Wildlife-Biology on 29 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

ORIGINAL ARTICLES

Effects of small mammal cycles on productivity of boreal ducks

Rodney W. Brook, David C. Duncan, James E. Hines, Suzanne Carrière & Robert G. Clark

Brook, R.W., Duncan, D.C., Hines, J.E., Carrière, S. & Clark, R.G. 2005: Effects of small mammals cycles on productivity of boreal ducks. - Wildl. Biol. 11: 3-11.

North American boreal nesting waterfowl (and their eggs and ducklings) share a number of generalist predators with small mammals and non-migratory birds that could indirectly link fluctuations in these coexisting prey. We surveyed pairs and broods to determine an index of productivity for lesser scaup *Aythya affinis* breeding near Yellowknife, Northwest Territories, Canada. We also calculated a mallard *Anas platyrhynchos* productivity index for birds from northern Saskatchewan, Canada. Small mammal abundance was estimated by snap trapping rodents and by counting pellets of snowshoe hares *Lepus americanus* in the Yellowknife area. Because small mammal data were not available for the same area as mallard harvest survey data, correlation with an estimate of ruffed grouse *Bonasa umbellus* harvest was used because small mammal abundance and grouse are known to correlate positively. We found a positive correlation between the abundance of rodents and lesser scaup productivity suggesting a prey switching relationship for predators between their main prey (rodents) and alternative prey (lesser scaup, eggs and ducklings). A negative correlation between snowshoe hare abundance and lesser scaup productivity was also found as well as a negative correlation between ruffed grouse abundance and mallard productivity. Negative correlations suggest a possible shared predation relationship, where changes in main prey abundance (hares) may cause a numerical response in predators that influences predation rates of shared alternative prey (ducks, eggs and ducklings). Although our conclusions are based on correlations, they indicate that a great deal of variation in boreal duck productivity might be explained by the indirect effects of coexisting prey abundance. Further work is needed to determine causal mechanisms contributing to these relationships, the effect of cycles in small mammal populations and the overall importance of top-down predator regulation for regulating duck productivity in boreal forest.

Key words: boreal forest, lesser scaup, mallard, predator-prey cycles, snowshoe hare, rodents, waterfowl

Rodney W. Brook, Department of Biology, University of Saskatchewan, 112 Science Place, Saskatoon, Saskatchewan, Canada S7N 5E2 - e-mail: rod.brook @ec.gc.ca*
David C. Duncan, Canadian Wildlife Service, Environment Canada, 200 - 4999, 98 Ave., Edmonton, Alberta, Canada T6B 2X3 - e-mail: dave.duncan@ec.gc.ca
James E. Hines, Canadian Wildlife Service, Environment Canada, Suite 301 - 5204, 50th Ave., Yellowknife, Northwest Territories, Canada X1A 1E2- e-mail: jim.hines@ec.gc.ca

Downloaded From: https://complete.bioone.org/journals/Wildlife-Biology on 29 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

Suzanne Carrière, Department of Resources, Wildlife and Economic Development, Government of the Northwest Territories, 600 - 5102, 50th Ave., Yellowknife, Northwest Territories, Canada X1A 3S8 - e-mail: Suzanne_carriere @gov.nt.ca
Robert G. Clark, Canadian Wildlife Service, Environment Canada, 115 Perimeter Road, Saskatoon, Saskatchewan, Canada S7N 0X4 - e-mail: bob.clark @ec.gc.ca

**Present address: 49 Camelot Drive, Ottawa, Ontario K1A OH3, Canada*

Corresponding author: Rodney W. Brook

Received 1 July 2003, accepted 22 January 2004

Associate Editor: Henrik Andrén

Waterfowl abundance and breeding success fluctuate synchronously with changes in the abundance of small mammals in arctic ecosystems (Pehrsson 1986, Summers & Underhill 1987, Wilson & Bromley 2001). Similar patterns have been reported on the North American prairies where duck productivity correlates positively with rodent densities (Byers 1974, Weller 1979, Crabtree & Wolfe 1988, Ackerman 2002). Top-down prey regulation by shared predators is most often hypothesized as the main mechanism linking fluctuations in abundance of small mammal populations and duck productivity (e.g. Greenwood 1987, Wilson & Bromley 2001, Ackerman 2002). In such relationships, one prey type affects predator abundance and behavioural response, which indirectly influences predation on another prey type (Holt 1977, Holt & Lawton 1994). Indirect effects on waterfowl productivity can be manifested through predators switching prey types (Lack 1954, Angelstam et al. 1984), sharing prey types (Norrdahl & Korpimäki 2000), by changing prey encounter rates (Schmidt 1999), or other intrinsic and extrinsic mechanisms (see Batzli 1996).

To our knowledge, there are no reports linking boreal breeding duck productivity to fluctuation in coexisting prey abundance, particularly within the well-known North American 10-year boreal cycle (e.g. Lack 1954, Keith 1963, Boutin et al.1995, King & Schaffer 2001, and references therein). The 10-year cycle is one of the most striking and ecologically dominating features of the boreal forest (Krebs et al. 2001a) where most animal populations fluctuate predictably every 8-13 years (Keith 1963, Keith 1990, Krebs et al. 1986). These fluctuations are driven by interactions among numbers of the keystone herbivore, snowshoe hare *Lepus americanus* (Begon et al. 1990, Boutin et al. 1995), their food supply and predators (Lack 1954, Keith 1963, Krebs et al. 1995, Vaughan & Keith 1981, Krebs et al. 2001a, Krebs et al. 2001c).

Although the relationship between hares and lynx *Lynx canadensis* is the best understood aspect of the cycle (Moran 1953), several other boreal forest vertebrates, both predator and prey, fluctuate with the abundance of hares (Keith & Cary 1991, Doyle & Smith 1994, Boutin et al. 1995, Krebs et al. 2001c). Grouse populations cycle with hares (Angelstam et al. 1984, Hannon et al. 1998, Martin et al.2001), declining one to two years prior to hares (Keith & Rusch 1988). Vole (*Microtus* spp. and *Clethrionomys* spp.) populations, however, appear to fluctuate independently from hare abundance (Gilbert & Krebs 1991, Gilbert et al. 1986, Boutin et al. 1995, Krebs et al. 2001c) and, in some areas, vole numbers correlate with the abundance of predators such as weasels *Mustela* spp. and northern hawk owls *Surnia ulula* (Rohner et al. 1995, Boutin et al. 1995).

In boreal forest, generalist predators are known to prey on small mammals, forest birds and waterfowl. For example, the red fox *Vulpes vulpes* feeds on rodents, snowshoe hares, grouse (Voight 1987, Banfield 1974) and nesting waterfowl and their eggs (Sargeant 1978, Cowardin et al. 1985). Red fox also fluctuate synchronously with prey abundance (Finerty 1980, Lindström 1980, Jones & Theberge 1983) and may link fluctuations in boreal prey populations. Our objective was to determine whether productivity of lesser scaup *Aythya affinis* and mallards *Anas platyrhynchos* was correlated with coexisting prey abundance in boreal forest of western Canada following the predictions of top-down predator regulation on coexisting prey in the 10-year boreal cycle.

Downloaded From: https://complete.bioone.org/journals/Wildlife-Biology on 29 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

Material and methods

Lesser scaup and small-mammal surveys

Breeding adult scaup were surveyed in mid-May and mid-June, 1989-2001 near Yellowknife, Northwest Territories, Canada. The Yellowknife Study Area (YKSA) is located in subarctic taiga and is described by Fournier & Hines (1999). During each survey, field crews visited all ponds and wetlands on the study area between 06:00 and 10:00 during a three-day period. Large ponds were surveyed by canoe. Scaup were recorded as alone, paired or grouped (Trauger 1971), and the number of indicated pairs was estimated following Dzubin (1969). As scaup population sex ratios are male biased (Allen et al. 1999) we used the estimated sex ratio from the May survey to improve the accuracy of estimated scaup pairs for the June survey by adjusting the mid-June survey results for paired males that may have mistakenly been recorded as lone males. As females are most vulnerable to mortality while nesting, we assumed little or no mortality bias in the sex ratio correction because the mid-June survey was sufficiently early in the breeding season that few nests were initiated (Brook 2002), and little or no female mortality had yet occurred.

Broods and the number of ducklings of each age class (Gollop & Marshall 1954) were counted during surveys conducted in good weather in mid-July and mid-August following the same methods as pair surveys. The number of broods was corrected for possible double counting in the two surveys based on duckling age class estimated from their size and feather appearance (Gollop & Marshall 1954). A visibility correction was not applied to pair or brood counts because they were considered highly visible, and visibility probably did not vary annually.

Abundance for rodent species was estimated using snap-trap transects in August from 1991 to 2000 (Shank 1997, Carrière 1998). The number of rodents captured per trap-night (corrected for misfires and non-target species) was used as an index of abundance. For hares, counts of faecal pellets were conducted in August of every year from 1988 to 2000, except 1997 and 1998, following the methods of Krebs et al. (2001b). Hare densities were estimated from the known relationship between hare numbers and pellet counts using functional (log-log) regression corrected for bias (Krebs et al. 2001b). This pellet count method estimated the mean density of hares/ha for the year preceding the count. Both snap-trapping and pellet counts for the Yellowknife station were done within 50 km of YKSA. Indices of hare and rodent abundance were also estimated for other boreal forest locations in the Northwest Territories

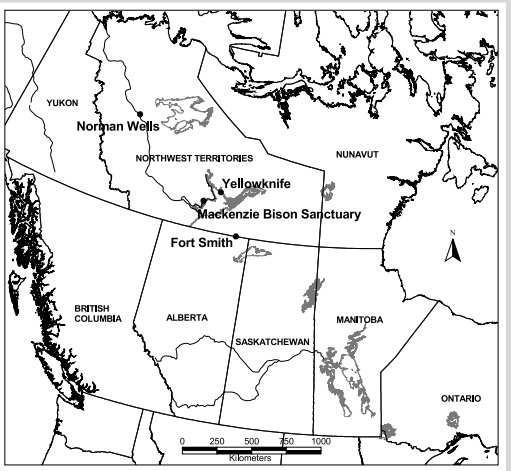


Figure 1. Sampling locations (•) for small mammal trapping and hare pellet counts, lesser scaup surveys (Yellowknife) and mallard and ruffed grouse harvest surveys (Northern Saskatchewan).

(Fort Smith, the Bison Sanctuary near Fort Providence and Norman Wells) using the same methods as above (Fig. 1).

We conducted a correlation (Pearson correlation: PROC CORR; SAS Institute Inc. 1990) and regression analysis on annual indices of rodent abundance (PROC GLM; SAS Institute Inc. 1990) and hare density (Geometric Mean Regression; Sokal & Rohlf 1995: 544) with estimates of scaup productivity. We used geometric mean regression because there was relatively large error in estimates of hare density (Krebs et al. 2001b) violating assumptions of model 1 linear regression (Sokal & Rohlf 1995:456). Second order polynomials were also tested in regressions to determine if relationships were curvilinear. Rodent abundance was a composite index of red-backed voles *Clethrionomys* spp., meadow voles *Microtus* spp. and deer mouse *Peromyscus maniculatus* numbers. Both species of voles were included in the index because they share common habitats and predator species (Banfield 1974). Deer mice were included in the index because voles and deer mice were correlated ($r = 0.69$, $P = 0.02$, $N = 11$) and likely share some of the same predator species (Banfield 1974). Because predator-prey relationships might lag in their numerical or functional responses to main prey, zero, one and two-year time lags were analyzed. Partial correlations were performed to determine if a potential explanatory variable (e.g. hare abundance) explained more variation in the response variable (e.g. scaup productivity) when controlling for variation in another

Downloaded From: https://complete.bioone.org/journals/Wildlife-Biology on 29 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

potential variable (e.g. rodent index; Sokal & Rohlf 1995). We also examined correlations in small mammal abundance among different sites to determine if fluctuations were geographically synchronous.

Mallard harvest age-ratio periodicity and ruffed grouse *Bonasa umbellus* abundance indices

Mallard productivity was estimated for northern Saskatchewan, Canada (harvest zone 2; primarily boreal forest) by calculating an age ratio (yearling:adult) from wings of harvested birds. Data were provided by the Canadian Wildlife Service who conduct the species composition survey of the migratory birds national harvest survey (see Levesque & Collins 1999 for description of survey and zones). A ratio of hatch year:adult birds is assumed to provide an index of mallard productivity for this area even though some birds harvested may have originated from other areas. Mallard harvest data were available from 1972 to 2000.

Harvest information for ruffed grouse was available for Saskatchewan over the same time period (1972-2000) and was provided by Saskatchewan Environment's gamebird harvest survey. Harvest data were corrected for number of active hunters to provide a reliable (Cattadori et al. 2003) annual index of ruffed grouse abundance. Although the ruffed grouse data are for the entire province and not restricted to northern Saskatchewan, most ruffed grouse inhabit central and northern Saskatchewan overlapping the boreal region. Pearson correlation was used to determine if the index of mallard productivity was correlated to the index of ruffed grouse abundance. One and two-year mallard time-lag correlations were also tested. We examined data from Saskatchewan because the grouse data collected there were available over a longer time than for other provinces.

Results

Number of scaup pairs and broods varied annually and were not correlated ($r = 0.07$, $P = 0.81$, $N = 13$). Average number of breeding pairs was 246 (SE = 13) with the highest count (358) recorded in 1990 and the lowest

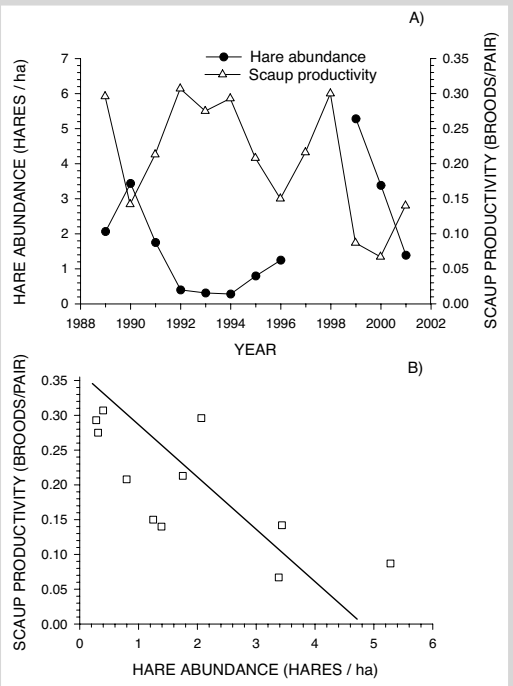


Figure 2. Indices of snowshoe hare abundance estimated from counts of faecal pellets near Yellowknife, Northwest Territories, Canada, during 1989-2000 and lesser scaup productivity (ratio of broods:pairs counted during surveys; A), and geometric mean regression ($\hat{y} = 0.36$ (SE = 0.07) - 0.07 (SE = 0.02)x; $r^2 = 0.56$) of lesser scaup productivity and snowshoe hare abundance (B).

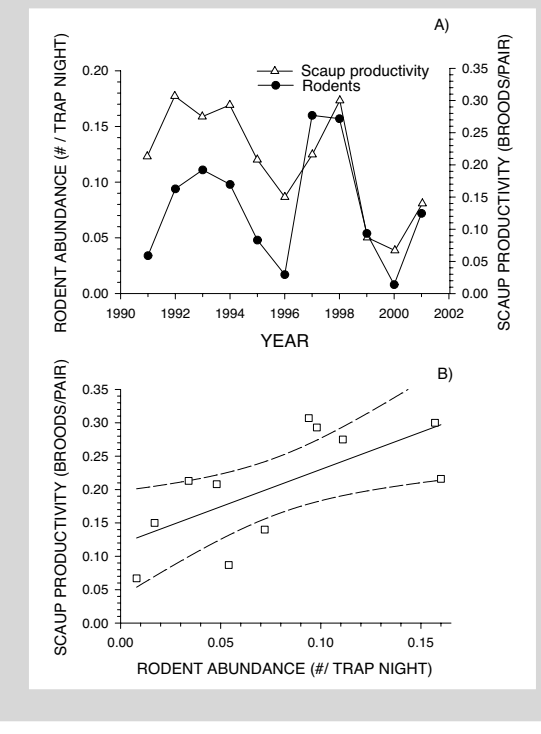


Figure 3. Annual indices of rodent abundance estimated from snap-trap transects near Yellowknife, Northwest Territories, Canada, during 1991-2000. The rodent index is a species composite including red-backed and meadow voles and deer mice. Lesser scaup productivity is estimated based on the ratio of broods to pairs counted on surveys (A). In B) regression ($y = 0.12 + 1.12x$); $r^2 = 0.46$) of the rodent abundance index and lesser scaup productivity is shown with 95% confidence limits (---).

Downloaded From: https://complete.bioone.org/journals/Wildlife-Biology on 29 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

(190) in 2001. Scaup productivity (ratio of broods to pairs) was much more variable, ranging from 0.07 in 2000 to 0.41 in 1992 (Fig. 2). Hare populations peaked in 1989-1990 and in 1999-2000. Indices of rodent density indicated peaks in 1993 and 1997-1998 (Fig. 3).

Correlation between scaup productivity and small mammal abundance

There was a significant negative correlation between the number of scaup broods per pair and hare density index for the Yellowknife site ($r = -0.75$, $P = 0.008$, $N = 11$) and a significant positive correlation between scaup production and the rodent index ($r = 0.68$, $P = 0.02$, $N = 11$). The correlation between scaup productivity and hare density was not improved by controlling for the correlation between scaup productivity and rodent abundance for those years when data were available for all indices (1991-1996, 1999 and 2000; $r = -0.83$, $P = 0.01$, $N = 9$ and partial $r = -0.78$, $P = 0.02$, $N = 9$). Similarly, controlling for variation in scaup productivity due to estimates of hare density did not improve the correlation between rodent abundance and scaup productivity ($r = 0.76$, $P = 0.02$, $N = 9$ and partial $r = 0.68$ $P = 0.06$, $N = 9$). Rodent abundance was not correlated with hare density ($r = -0.52$, $P = 0.16$, $N = 9$), and no time lag correlations were detected between hare density and scaup productivity. A two-year time lag correlation was detected between rodent abundance and scaup productivity (Table 1). Relationships were not curvilinear ($P > 0.05$).

Mallard and ruffed grouse harvest

Estimates of mallard age ratio from birds harvested in northern Saskatchewan averaged 2.17 yearlings per adult with a maximum (5.22) recorded in 1975 and minimum (0.31) in 1988. Ruffed grouse harvest per active hunter averaged 3.8 with a maximum (8.0) recorded in 1987 and a minimum (1.4) in 1973. Mallard productivity and grouse harvest were not directly correlated, but correlations were significant for one and two-year mallard time lags (Table 2).

Table 1. Correlation between estimates of lesser scaup productivity and indices of small mammal density in boreal forest near Yellowknife, Northwest Territories, Canada. The correlations are shown for zero (t), one (t + 1) and two-year (t + 2) time lags during 1989-2001. Sample size (N = years) is given in parentheses. The rodent index is a composite index of red-backed (*Clethrionomys* spp.) and meadow (*Microtus* spp.) voles, and deer mice *Peromyscus maniculatus*. *: $P < 0.05$

	Scaup productivity		
	t	t + 1	t + 2
Hare abundance	-0.75* (11)	-0.49 (11)	0.29 (10)
Rodent index	0.68* (11)	0.10 (10)	-0.76* (9)

Table 2. Correlation between estimates of mallard productivity and indices of ruffed grouse abundance in the boreal forest of northern Saskatchewan, Canada. Correlations are shown for zero (t; N = 29), one (t + 1; N = 28) and two-year (t + 2; N = 27) time lags during 1972-2000. *: $P < 0.05$.

	Grouse abundance		
	t	t + 1	t + 2
Mallard productivity	-0.11	-0.41*	-0.55*

Discussion

Boreal predators

Boreal predators and scavengers (egg predators) observed on the YKSA and in Northern Saskatchewan that could link fluctuations of coexisting prey populations include, but are not limited to, red fox, common raven *Corvus corax*, northern goshawk *Accipiter gentilis*, northern harrier *Circus cyaneus*, mink *Mustela vison* and great horned owl *Bubo virginianus*. Mink, a generalist boreal predator of small mammals, ducks and their eggs (Eagle & Whitman 1987, Banfield 1974) are reported to fluctuate in synchrony with abundance of prey (Keith & Cary 1991) similar to the red fox. Avian predators and scavengers like the northern goshawk (Doyle & Smith 1994), common raven (Doyle & Smith 2001) and great horned owl (Rohner et al. 2001) also feed on small mammals, forest birds, ducks and their eggs, with their abundance and reproduction similarly influenced by the abundance of snowshoe hares and other boreal small mammals.

Predator-prey relationships

Two hypotheses could explain the different correlative patterns observed. The shared predation hypothesis (Norrdahl & Korpimäki 2000) proposes that predators have a numerical population response to main prey density change which cause an indirect effect on predation rates of alternative prey. Predators kill main and alternative prey unselectively and could cause a decline in alternative prey density before main prey populations begin to decline (Kenward 1985, Newton 1998, Norrdahl & Korpimäki 2000).

The alternative prey hypothesis (Lack 1954, Angelstam et al. 1984) suggests a decline in predation rate of alternative prey as main prey density increases. Predators shift to main prey as they become more abundant thus buffering the predation rate on alternative prey. As main prey become scarce, predators shift back to alternative prey. Characteristics of both predation hypotheses may explain the correlative relationships we observed between main prey abundance and waterfowl productivity.

Consistent with the shared predation hypothesis, scaup

Downloaded From: https://complete.bioone.org/journals/Wildlife-Biology on 29 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

productivity was negatively correlated with hare density, possibly because generalist predators were more abundant during periods of high hare populations. The predation rate on scaup and their eggs may be highest as hare populations increase or peak as a result of the numerical response of predators to main prey. This mechanism is also thought to explain the decline of ruffed grouse (alternative prey) before the decline in snowshoe hare abundance (Keith 1963, Keith & Rusch 1988 in Norrdahl & Korpimäki 2000).

Supportive evidence for the shared predation hypothesis was observed in the correlation between ruffed grouse abundance (Fig. 4) and mallard productivity in Northern Saskatchewan. Even though these did not correlate directly, we hypothesized a direct correlation between mallard productivity and snowshoe hare abundance (which was unavailable), and by extension, a time-lag correlation between mallard productivity and ruffed grouse because predator populations are likely regulated by fluctuations in hares (Begon et al. 1990). Some grouse populations are cyclical (Angelstam et al. 1984, Lindström et al. 1996, Hannon et al. 1998, Martin et al. 2001) and decline one to two years prior to hares (Keith & Rusch 1988) exhibiting evidence for the shared predation hypothesis. Therefore a time lag in the correlation between mallard productivity and ruffed grouse abundance was expected.

We tested for time lag correlations between scaup productivity and hare abundance to determine if there was a lag in predator numerical response to main prey population change (Begon et al. 1990) that is reflected in the alternative prey population. Boutin et al. (1995) found time lag correlations between hare density and abundance of two predators, northern goshawks and great horned owls in the Yukon, Canada. We found no time lag between hare density and scaup productivity but our data are likely of insufficient duration to detect a lag.

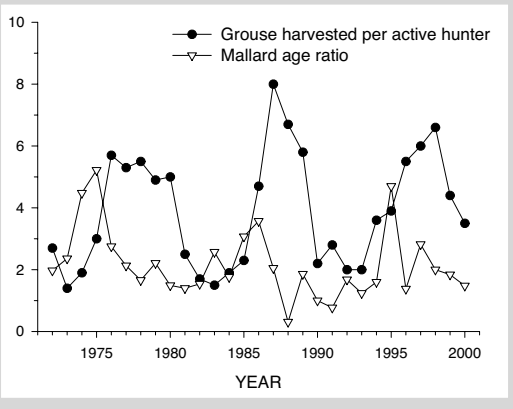


Figure 4. Annual indices of mallard age-ratio (hatch year:adult) and ruffed grouse harvest (per active hunter) for northern Saskatchewan, Canada, during 1972-2000.

The positive correlation between rodent abundance and scaup productivity is characteristic of the alternative prey hypothesis. When rodents (main prey) are plentiful, nesting female ducks and their eggs may be buffered from predation. When rodents are scarce, alternative prey are no longer buffered from predation and predation rates increase. This could occur through either chance encounter of all prey from changing predator search time or through active prey switching. The phenomenon has been most commonly reported for arctic ecosystems where specialist predators (e.g. arctic fox *Alopex lagopus*) of lemmings *Lemmus* spp. and *Dicrostonyx* spp. switch to alternative prey (nesting birds and their eggs) when lemmings are scarce (Pehrsson 1986, Summers & Underhill 1987, Underhill et al. 1993, Bêty et al. 2001, Wilson & Bromley 2001).

A strongly negative two-year time lag correlation was found between the rodent composite index and the index of scaup productivity. However, the significant time lag correlation found is likely an artifact caused by the 3-5 year periodicity of the rodent cycle (Boutin et al. 1995, Norrdahl & Korpimäki 2000, our study). The two-year time lag (half the cycle length) produced a strong negative correlation when there was a strong positive correlation for zero time lag.

Our observations do not allow a rigorous test of both hypotheses though our results are consistent with predictions of both. If predation is the main mechanism linking fluctuations in the hare and rodent populations with waterfowl productivity then we suspect the predator communities exploiting the two main prey types are different and have different response to change in density of these two main prey types with respect to their effects on alternative prey. Conversely, its also likely the two main prey types have predator species in common. More direct study of the dynamics of the boreal predator community are needed to help further understand the mechanisms that influence boreal waterfowl productivity.

Synchrony of small mammal cycles

Populations of rodents in the boreal region appear to be cyclic, fluctuating at 3-5 year intervals independently of the 8-13 year hare cycle (Boutin et al. 1995, our study). Lindén (1988) reports similar cycle lengths for rodents and mountain hare *L. timidus* in Finland though the 10-year cycle in Europe is not as pronounced as in North America. Further, evidence for the 10-year predator-prey

Downloaded From: https://complete.bioone.org/journals/Wildlife-Biology on 29 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

Table 3. Correlation matrix of annual indices of snowshoe hare density and rodent abundance for four and three locations, respectively, in boreal forest, Northwest Territories, Canada. Hare density is estimated from counts of faecal pellets during 1989-2001, and the rodent index is a composite index of red-backed (*Clethrionomys* spp.) and meadow (*Microtus* spp.) voles, and deer mice *Peromyscus maniculatus* indexed using snap traps during 1991-2001. The rodent index was not available (n.a.) for the Mackenzie Bison Sanctuary. Sample size (N = years) is given in parentheses. *: $P < 0.01$.

Location	Forth Smith	Norman Wells	Mackenzie Bison Sanctuary	Yellowknife
Snowshoe hare				
Fort Smith	1.00	0.75 (11)*	0.75 (11)*	0.76 (10)*
Norman Wells		1.00	0.34 (11)	0.89 (10)*
Sanctuary			1.00	0.37 (10)
Yellowknife				1.00
Rodent				
Fort Smith	1.00	0.44 (10)	n.a.	0.11 (11)
Norman Wells		1.00		0.04 (10)
Yellowknife				1.00

cycle was observed in the indices of productivity for another migratory bird, the whooping crane *Grus americana* nesting in boreal forest (Boyce & Miller 1985).

Our analyses suggest that scaup productivity was correlated with rodent abundance independent of the correlation with hare abundance. From this scant evidence, we cannot determine how these two apparently independent cycles interact with each other and the predator community, however, synchrony of mammal cycles over large geographical areas may have a greater impact on the variability of continental duck populations than if synchrony were lacking, assuming a cause and effect relationship. Estimates of hare density were highly correlated among several locations though correlation does not appear to be related to distance (Table 3, see Fig. 1) as others found (Lindström et al. 1996). No synchrony was detected with the rodent index suggesting the rodent cycle may make less of an indirect impact on continental waterfowl populations. Evidence for a potential cyclical effect of predation on boreal ducks, their eggs and young may explain a significant amount of the variation in boreal duck productivity. However, correlation does not equal causation and other potential mechanisms in addition to top-down predator regulation need to be assessed for boreal waterfowl production. For example, annual variability in food supply and environmental and habitat conditions (e.g. Pehrsson 1986, Pietz et al. 2000) could directly affect small mammals and ducks. Further (experimental) tests of factors influencing waterfowl survival and reproduction in boreal forest are needed.

Acknowledgements - we thank all the staff from various agencies and all the field assistants too numerous to mention. Small mammal data were provided by the NWT small mammal urvey, which was made possible by numerous wildlife officers, biologists and volunteers. We acknowledge D. McKinnon of Saskatchewan Environment for graciously providing ruffed grouse data. We thank A. Darwin for providing figure 1. The manuscript was greatly improved by comments from K. Ross and Johan Elmberg. Funding for the productivity work was provided by the Canadian Wildlife Service, University of Saskatchewan, Department of Biology, Natural Sciences and Engineering Research Council of Canada (through grants to Robert G. Clark) and Indian and Northern Affairs Canada, Northern Scientific Training Program.

References

Ackerman, J.T. 2002: Of mice and mallards: positive indirect effects of coexisting prey on waterfowl nest success. - Oikos 99: 469-480.

Allen, G.T., Caithamer, D.F. & Otto, M. 1999: A review of the status of greater and lesser scaup in North America. - U.S. Fish and Wildlife Service, Arlington, Virginia, USA, 45 pp.

Angelstam, P., Lindström, E. & Widén, P. 1984: Role of predation in short-term population fluctuations of some birds and mammals in Fennoscandia. - Oecologia 62: 199-208.

Banfield, A.W.F. 1974: The mammals of Canada. - University of Toronto Press, Toronto, Ontario, Canada, 438 pp.

Batzli, G.O. 1996: Population cycles revisited. - Trends in Ecology and Evolution 11: 488-489.

Begon, M., Harper, J.L. & Townsend, C.R. 1990: Ecology: individuals, populations and communities. - Oxford, Blackwell Scientific Publications, Cambridge, Massachusetts, USA, 945 pp.

Bêty, J., Gauthier, G., Giroux, J-F. & Korpimäki, E. 2001: Are goose nesting success and lemming cycles linked? Interplay between nest density and predators. - Oikos 93: 388-400.

Boutin, S., Krebs, C.J., Boonstra, R., Dale, M.R.T, Hannon, S.J., Martin, K., Sinclair, A.R.E, Smith, J.N.M., Turkington, R., Blower, M., Byrom, A., Doyle, F.I., Doyle, C., Hik, D., Hofer, L., Hubbs, A., Karels, T., Murray, D.L., Nams, V., O'Donoghue, M., Rohner, C. & Schweiger, S. 1995: Population changes of the vertebrate community during a snowshoe hare cycle in Canada's boreal forest. - Oikos 74: 69-80.

Downloaded From: https://complete.bioone.org/journals/Wildlife-Biology on 29 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

Boyce, M.S. & Miller, R.S. 1985: Ten-year periodicity in whooping crane census. - Auk 102: 658-660.

Brook, R.W. 2002: Breeding ecology and local population dynamics of lesser scaup (Aythya affinis) in boreal forest of western Canada. - M.Sc. thesis, University of Saskatchewan, Saskatoon, Saskatchewan, Canada, 108 pp.

Byers, S.M. 1974: Predator-prey relationships on an Iowa waterfowl nesting area. - Transactions of the North American Wildlife and Natural Resources Conference 39: 223-229.

Carrière, S. 1998: Small mammal survey in the Northwest Territories and Nunavut - Report 1998. Manuscript report 115, Government of the Northwest Territories, Department of Resources, Wildlife and Economic Development, Yellowknife, Northwest Territories, Canada, 22 pp.

Cattadori, I.M., Haydon, D.T., Thirgood, S.J. & Hudson, P.J. 2003: Are indirect measures of abundance a useful index of population density? The case of red grouse harvesting. - Oikos 100: 439-446.

Cowardin, L.M., Gilmer, D.S. & Shaiffer, C.W. 1985: Mallard recruitment in the agricultural environment of North Dakota. - Wildlife Monograph 92, 37 pp.

Crabtree, R.L. & Wolfe, M.L. 1988: Effects of alternative prey on skunk predation of waterfowl nests. - Wildlife Society Bulletin 16: 163-169.

Doyle, F.I. & Smith, J.N.M. 1994: Population responses of northern goshawks to the 10-year cycle in number of snowshoe hares. - Studies in Avian Biology 16: 122-129.

Doyle, F.I. & Smith, J.N.M. 2001: Raptors and scavengers. - In: Krebs, C.J., Boutin, S. & Boonstra, R. (Eds.); Ecosystem dynamics of the boreal forest: The Kluane project. Oxford University Press, New York, New York, USA, pp. 377-404.

Dzubin, A. 1969: Assessing breeding populations of ducks by ground counts. Saskatoon Wetlands Seminar. - Canadian Wildlife Service Report Series 6: 178-230.

Eagle, T.C. & Whitman, J.S. 1987: Mink. - In: Novak, M., Baker, J.A., Obbard, M.E. & Malloch, B. (Eds.); Wild furbearer management and conservation in North America. Ministry of Natural Resources, Ontario, Canada, pp. 614-624.

Finerty, J.P. 1980: The population ecology of cycles in small mammals: mathematical theory and biological fact. - Yale University Press, New Haven, Connecticut, 234 pp.

Fournier, M.A. & Hines, J.E. 1999: Breeding ecology of horned grebe Podiceps auritus in subarctic wetlands. - Canadian Wildlife Service Occasional Paper 99, Ottawa, Ontario, Canada, 32 pp.

Gilbert, B.S. & Krebs, C.J. 1991: Population dynamics of Clethrionomys and Peromyscus in southwestern Yukon 1973-1989. - Holarctic Ecology 14: 250-259.

Gilbert, B.S., Krebs, C.J., Talarico, D. & Cichowski, D.B. 1986: Do Clethrionmys rutilus females suppress maturation of juvenile females? - Journal of Animal Ecology 55: 543-552.

Gollop, J.B. & Marshall, W.H. 1954: A guide for aging duck broods in the field. - Mississippi Flyway Council Technical Section (mimeo), Canadian Wildlife Service, unpublished report, Ottawa, Ontario, 14 pp.

Greenwood, J.J.D. 1987: Three-year cycles of lemmings and Arctic geese explained. - Nature 328: 577.

Hannon, S.J., Eason, P. & Martin, K. 1998: The Willow Ptarmigan. - In: Poole, A. & Gill, F. (Eds); The Birds of North America. No. 369. - The Birds of North America, Inc., Philadelphia, Pennsylvania, USA, 28 pp.

Holt, R.D. 1977: Predation, apparent competition and the structure of prey communities. - Theoretical Population Biology 12: 197-229.

Holt, R.D. & Lawton, J.H. 1994: The ecological consequences of shared natural enemies. - Annual Review of Ecology and Systematics 25: 495-520.

Jones, D.M. & Theberge, J.B. 1983: Variation in red fox, Vulpes vulpes, summer diets in northwest British Columbia and southwest Yukon. - Canadian Field Naturalist 97: 311-314.

Keith, L.B. 1963: Wildlife's ten-year cycle. - University of Wisconsin Press, Madison, Wisconsin, USA, 201 pp.

Keith, L.B. 1990: Dynamics of snowshoe hare populations. - In: Genoways, H.H. (Ed); Current mammalogy. Plenum Press, New York, New York, USA, pp. 119-195.

Keith, L.B. & Cary, J.R. 1991: Mustelid, squirrel, and porcupine population trends during a snowshoe hare cycle. - Journal of Mammalogy 72: 373-378.

Keith, L.B. & Rusch, D.H. 1988: Predation's role in the cyclic fluctuations of ruffed grouse. - Acta XIX Congressus Internationalis Ornithologici, Ottawa, Ontario, Canada 1986, pp. 699-732.

Kenward, R.E. 1985: Problems of goshawk predation on pigeons and other game. - Proceedings of the International Ornithological Congress 18: 666-678.

King, A.A. & Schaffer, W.M. 2001: The geometry of a population cycle: A mechanistic model of snowshoe hare demography. - Ecology. 82: 814-830.

Krebs, C.J., Boonstra, R., Boutin, S. & Sinclair, A.R.E. 2001a: What drives the 10-year cycle of snowshoe hares? - BioScience 51: 25-35.

Krebs, C.J., Boonstra, R., Boutin, S., Sinclair, A.R.E., Smith, J.N.M., Dale, M.R.T., Martin, K. & Turkington, R. 1995: Impact of food and predation on the snowshoe hare cycle. - Science 269: 1112-1115.

Krebs, C.J., Boonstra, R., Nams, V., O'Donoghue, M., Hodges, K.E. & Boutin, S. 2001b: Estimating snowshoe hare population density from pellet plots: a further evaluation. - Canadian Journal of Zoology 79: 1-4.

Krebs, C.J., Boutin, S. & Boonstra, R. 2001c: Ecosystem dynamics of the boreal forest: The Kluane project. - Oxford University Press, New York, New York, USA, 511 pp.

Krebs, C.J., Gilbert, B.S., Boutin, S., Sinclair, A.R.E. & Smith, J.N.M. 1986: Population biology of snowshoe hares. I. Demography of food-supplemented population in the southern Yukon, 1976-84. - Journal of Animal Ecology 55: 963-982.

Lack, D. 1954: The natural regulation of animal numbers. - Clarendon Press, Oxford, 343 pp.

Levesque, H. & Collins, B. 1999: Migratory game birds harvested in Canada during the 1991, 1992, and 1993 hunting seasons. - Canadian Wildlife Service Progress Note 214, Ottawa, Ontario, Canada, 3 pp.

Downloaded From: https://complete.bioone.org/journals/Wildlife-Biology on 29 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

Lindén, H. 1988: Latitudinal gradients in predator-prey interactions cyclicity and synchronism in voles and small game populations in Finland. - Oikos 52: 341-349.

Lindström, E. 1980: The red fox in a small game community of the south taiga region in Sweden. - In: Zimen, E. (Ed.); The red fox. Biogeographica Vol. 18, The Hague, The Netherlands, pp. 177-184.

Lindström, E., Ranta, E. & Lindén, H. 1996: Large-scale synchrony in the dynamics of capercaillie, black grouse and hazel grouse populations in Finland. - Oikos 76: 221-227.

Martin, K., Doyle, C., Hannon, S.J. & Mueller, F. 2001: Forest grouse and ptarmigan. - In: Krebs, C.J., Boutin, S. & Boonstra, R. (Eds.); Ecosystem dynamics of the boreal forest: The Kluane project. Oxford University Press, New York, New York, USA, pp. 240-260.

Moran, P.A.P. 1953: The statistical analysis of the Canadian lynx cycle. - Australian Journal of Zoology 1: 291-298.

Newton, I. 1998: Population limitation in birds. - Academic Press, San Diego, California, USA, 597 pp.

Norrdahl, K. & Korpimäki, E. 2000: Do predators limit the abundance of alternative prey? Experiments with vole-eating avian and mammalian predators. - Oikos 91: 528-540.

Pehrsson, O. 1986: Duckling production of the Oldsquaw in relation to spring weather and small-rodent fluctuations. - Canadian Journal of Zoology 64: 1835-1841.

Pietz, J.P., Krapu, G.L., Buhl, D.A. & Brandt, D.A. 2000: Effects of water conditions on clutch size, egg volume, and hatchling mass of mallards and gadwalls in the prairie pothole region. - Condor 102: 936-940.

Rohner, C.J., Doyle, F.I. & Smith, J.N.M. 2001: Great horned owls. - In: Krebs, C.J., Boutin, S. & Boonstra, R. (Eds.); Ecosystem dynamics of the boreal forest: The Kluane project. Oxford University Press, New York, New York, USA, pp. 340-376.

Rohner, C.J., Smith, J.N.M., Stroman, J. & Joyce, M. 1995: Northern hawk-owls in the nearctic boreal forest: Prey selection and population consequences of multiple prey cycles. - Condor 97: 208-220.

Sargeant, A.B. 1978: Red fox prey demands and implications to prairie duck production. - Journal of Wildlife Management 42: 520-527.

SAS Institute Inc. 1990: SAS/STAT user's guide, Version 6. 4th edition - SAS Institute Inc., Cary, North Carolina, USA, 1686 pp.

Schmidt, K.A. 1999: Foraging theory as a conceptual framework for studying nest predation. - Oikos 85: 151-160.

Shank, C.C. 1997: The Northwest Territories small mammal survey: 1990-1996. - Manuscript report 96, Government of the Northwest Territories, Department of Resources, Wildlife and Economic Development, Yellowknife, Northwest Territories, Canada, 25 pp.

Sokal, R.R. & Rohlf, F.J. 1995: Biometry. Third Edition. - W.H. Freeman and Company, New York, New York, USA, 887 pp.

Summers, R.W. & Underhill, L. 1987: Factors related to breeding production of brent geese Branta b. bernicla and waders (Charadrii). - Bird Study 37: 161-171.

Trauger, D.L. 1971: Population ecology of lesser scaup (Aythya affinis) in subarctic taiga. - PhD thesis, Iowa State University, Ames, Iowa, USA, 118 pp.

Underhill, L.G., Prys-Jones, R.P., Syroechkovski, E.E., Groen, N.M., Karpov, V., Lappo, H.G., Van Roomen, M.W.J., Rybkin, A., Schekkerman, H., Spiekman, H. & Summers, R.W. 1993: Breeding of waders (Charadrii) and brent geese Branta bernicla bernicla at Pronchishcheva Lake, northeastern Taimyr, Russia, in a peak and a decreasing lemming year. - Ibis 135: 277-292.

Vaughan, M.R. & Keith, L.B. 1981: Demographic response of experimental snowshoe hare populations to over-winter food shortage. - Journal of Wildlife Management 45: 354-380.

Voight, D.R. 1987: Red fox. - In: Novak, M., Baker, J.A., Obbard, M.E. & Malloch, B. (Eds.); Wild furbearer management and conservation in North America. Ministry of Natural Resources, Ontario, Canada, pp. 614-624.

Weller, M.W. 1979: Density and habitat relationships of blue-winged teal nesting in Northwestern Iowa. - Journal of Wildlife Management 43: 367-374.

Wilson, D. & Bromley, R. 2001: Functional and numerical responses of predators to cyclic lemming abundance: effects on loss of goose nests. - Canadian Journal of Zoology 79: 525-532.

Downloaded From: https://complete.bioone.org/journals/Wildlife-Biology on 29 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use