Morphological responses of white-tailed deer to a severe population reduction

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Abstract: We document responses, in terms of mass, hind-foot length, and antler beam diameter, of white-tailed deer (*Odocoileus virginianus borealis*) to an approximate 85% population reduction achieved by means of a series of public hunts in Long Point National Wildlife Area (LPNWA), Lake Erie, Ontario. Dressed weights and yearling antler beam diameters of LPNWA deer are among the lowest on record for this subspecies. Notable increases between 1989 and 1990 and in 1994 were common, especially in younger animals. Most significantly ($P \leq 0.05$), from 1989 to 1994, mean mass of male fawns increased by 44%, that of yearling males by 96%, and that of 2.5-year-old bucks by 75%. Significant increases in mean hind-foot length were also noted in male and female fawns and 2.5-year-old bucks. Antler beam diameters increased by 93% in yearlings and 35% in 2.5-year-old bucks between 1989 and 1994. The significant and immediate responses to decreased density and competition demonstrate that the herd was under extreme environmental stress and show the exceptional resiliency of this species in withstanding severe environmental pressure. Long Point deer are not genetically smaller than adjacent mainland deer as some had thought, but their growth has been restricted by environmental conditions.

Résumé : On trouvera ici les résultats d'une étude de la masse, de la longueur du pied arrière et du diamètre du merrain chez des Cerfs de Virginie (*Odocoileus virginianus borealis*) après une diminution d'environ 85% de la population à la suite d'une série de chasses ouvertes dans la réserve faunique nationale de Long Point (LPNWA), lac Érié, Ontario. La masse des carcasses sans les viscères et le diamètre du merrain chez les jeunes de 1 an de cette population étaient parmi les plus faibles jamais enregistrés chez cette sous-espèce. Entre 1989 et 1990 et 1994, des augmentations appréciables ont été enregistrées, surtout chez les jeunes cerfs. L'augmentation la plus significative ($P \leq 0,05$) a été celle de la masse entre 1989 et 1994, de 44% chez les faons mâles, de 96% chez les mâles de 1 an et de 75% chez les mâles adultes de 2,5 ans. La longueur moyenne du pied arrière a également augmenté significativement chez les faons mâles et femelles et chez les mâles adultes de 2,5 ans. Entre 1989 et 1994, le diamètre du merrain a augmenté de 93% chez les jeunes de 1 an et de 35% chez les mâles de 2,5 ans. La réaction significative et immédiate de la population à la diminution de la densité et de la compétition indique que le troupeau était soumis à un stress environnemental extrême et illustre la capacité exceptionnelle de cette espèce de survivre à des pressions environnementales très rigoureuses. Les cerfs de ce troupeau ne sont pas génétiquement plus petits que ceux des populations continentales adjacentes, mais leur croissance a été entravée par les conditions du milieu.
[Traduit par la Rédaction]

Introduction

The body morphology of white-tailed deer (*Odocoileus virginianus*) are one of the foremost means by which it responds to its environment. Although the relationships between mass (Mackie 1964; Severinghaus 1979; Dickinson 1983; Sweet and Wright 1952; Kie et al.1983; Jacobson 1984), skeleton size (Klein 1964), antler growth (Cowan and Long 1962; McCullough 1982), and range condition have been well documented, the comparisons have been mostly of disparate herds and ranges. Some studies (McCullough 1979; Leberg and Smith 1993) have tracked the same populations over time, but conditions have not been comparable to the extremes in density or response presented here. We document the morphological responses of a free-ranging herd of white-tailed deer to an approximate 85% reduction in population over a 5-year period in the chronically overpopulated Long Point National Wildlife Area (LPNWA) in southern Ontario.

The herd reduction was effected by a series of controlled public hunts from 1989 to 1994 held as part of a management program designed to promote the regeneration of severely overbrowsed habitat. Overbrowsing on LPNWA has been documented since 1931 (Snyder and Logier 1931) and has resulted in the virtual absence of understorey trees and shrubs (McCullough and Robinson 1988). Based on browsable biomass of preferred browse species, the carrying capacity of the winter range in LPNWA in 1993 was estimated to be between 35 and 42 animals (Ashley 1993).[1] Prior to the 1989 hunt there were approximately 500 deer wintering on LPNWA. For several decades the Long Point herd has depleted the deciduous woody shrub and tree species across its entire range, and during the wintering period has subsisted on a diet of poor-quality browse, primarily ground juniper (*Juniperus communis depressa*), red-cedar (*Juniperus virginianus*), tamarack (*Larix laricina*), grasses, and forbs. The abundance of poor-quality browse supplemented by herbaceous plants,

[1] E.P. Ashley. 1993. An assessment of white-tailed deer winter browse conditions and carrying capacity, Long Point, 1993. Unpublished report, Canadian Wildlife Service, Long Point National Wildlife Area, R.R.3, Port Rowan, ON N0E 1M0, Canada.

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and moderate winters due to lake effect, helped to sustain the population at a level well above the carrying capacity of preferred browse species.

Study area

Long Point is a 32-km 6450-ha sandspit on the north shore of Lake Erie, centred at 80°12'W, 42°33'N in the Regional Municipality of Haldimand–Norfolk, Ontario. The peninsula runs northwest to southeast, projecting almost to the centre of Lake Erie. Its maximum width is nearly 2 km. The uplands are a series of northeast–southwest rolling parallel sand ridges separated by various types of wetlands. In 1978 the eastern half of Long Point (3200 ha) was donated to the Canadian government by the Long Point Company, a private hunting club. The terms of the donation include restrictive covenants that limit public access and activities on the lands. The property is now managed as a National Wildlife Area by the Canadian Wildlife Service (CWS) of Environment Canada.

The vegetation communities of LPNWA are determined to a large extent by topography, soils, climate, past fires, and chronic overbrowsing by white-tailed deer (McCullough and Robinson 1988). Records indicate that the vegetation composition was once very different. Charlevoix (1776) stated that the Point "naturally produces many vines" and Black (1854) referred to the cedar community of Long Point as a "dense jungle." By 1931 the LPNWA appears to have taken on a different appearance. Snyder and Logier (1931) reported that red-cedar was not as plentiful and that the peninsula had taken on its present day "park-like conditions." Several tree species mentioned by Snyder and Logier in 1931, beech (*Fagus grandifolia*), butternut (*Juglans cinerea*), high-bush cranberry (*Viburnum trilobum*), climbing bittersweet (*Celastrus scandens*), alternate-leaved dogwood (*Cornus alternifolia*), Virginia creeper (*Parthenocissus quinquefolia*), gooseberry (*Ribes* sp.), red raspberry (*Rubus idaeus*), blackberry (*Rubus occidentalis*), and witch hazel (*Hamamelis virginiana*), are rare or absent from the floral communities of LPNWA today (McCullough and Robinson 1988). Savannah-like conditions on the peninsula have been exacerbated by the activities of people. Much of the good timber on the Point was logged sporadically under a commercial licence or illegally from the 1850s to 1951 (McCullough and Robinson 1988). The development of savannah-like conditions was also aided by fires (Heffernan 1978).

Reznicek and Catling (1989) estimated that there are approximately 750 species of vascular plants on Long Point, but many shrubs and forbs common on the mainland are poorly represented. These authors attribute this to heavy overbrowsing by white-tailed deer. Forty-two provincially rare species, and 3 species found nowhere else in Canada, are present on the peninsula. Sixty species found on Long Point are rare in the rest of the Regional Municipality of Haldimand–Norfolk (Reznicek and Catling 1989).

Heffernan (1978) identified four forest communities (>50% canopy cover): white pine (*Pinus strobus*) – white cedar (*Thuja occidentalis*), birch (*Betula payrifera*) – red oak (*Quercus rubra*) – white pine, red oak – sugar maple (*Acer saccharum*), and tamarack – white cedar. Four savanna communities (<50% canopy cover) were also noted: cottonwood (*Populus deltoides*), red-cedar, oak–pine, and oak savannah. Other types of vegetation communities found on the peninsula include beach, dry dune, wetland, and aquatic communities (Reznicek and Catling 1989).

White-tailed deer are native to Long Point, having been reported as early as 1669 (McKeating 1983). By 1870 the herd had been extirpated by overhunting (Snyder and Logier 1931), but in the 1870s and 1880s, deer from Minnesota and Rondeau, Ontario, were released in order to reestablish the herd. Heffernan (1978) reported that by 1890, the herd "had greatly increased in numbers," and in 1927, Snyder and Logier (1931) observed that the herd was threatening its own food supply. There has been limited hunting since the land was purchased by a private waterfowl club in 1866, and most human activity on LPNWA, including deer hunting, has been prohibited since 1978.

Methods

Population estimates

The size of the LPNWA herd was estimated by means of winter drive counts in 1986 and 1988. Since 1990, snow and ice conditions have been unfavourable for winter counts. Estimates of natural mortality and recruitment based on the 1989 and 1990 age structure of harvested animals were used to estimate the population since 1990. The count in January 1986 produced a population estimate of 475 deer and another in 1988 gave a winter estimate of 500 deer, yielding a density of 62.5 deer/km^2 on the 800-ha wintering area. Based on this count, the 1989 prehunt population was estimated at 550 animals. In 1989, 405 deer were culled (a 74% reduction). In 1990, a winter drive count of 124 animals indicated a prehunt population of 156 deer. During the 1990 public hunt, 70 deer passed through check stations and an additional 15 animals were killed for Lyme disease research, yielding a total kill of 85 deer. From 1991 to 1994 an additional 15 deer were collected for a Lyme disease research project. Poor conditions, either thin ice, open water, or lack of beach access, have prevented the winter drive count of the herd since 1990. The 1994 prehunt population was estimated at 120 animals. Forty-two animals were harvested during the 1994 hunt.

Public hunt

Applicants were chosen by random draw and were required to apply and hunt as parties of 2–8. Participants were required to attend an information seminar prior to the hunt. Each hunter was allowed two deer, at least one of which had to be antlerless. Hunters were permitted to harvest up to the party limit of available tags and were required to use centre-fire rifles, shotguns, or muzzle-loaders. Six 2-day hunts were held in 1989 and three 3-day hunts in 1990 and 1994.

Morphometrics

All deer were processed at mandatory check stations operated by the CWS. The following variables were assessed: dressed (eviscerated) weight to the nearest 100 g (using a balance scale); hind-foot length from the proximal tip of the calcaneus to the most distal part of the extended hoof, to the nearest 1 mm (using a flexible steel tape); antler beam diameter, to the nearest 0.1 mm, taken as the average of two measurements taken at right angles 2.54 cm (1 in.) above the burr (using a vernier calliper); presence or absence of lactation, determined by examining the udder for milk; and age, from tooth eruption and wear (Severinghaus 1949). Mandibles were removed and incisors were later cementum-aged. All males aged 5.5 years and older are grouped as age-class 5.5+ and all females aged 4.5 years and older as age-class 4.5+.

Table 1. Dressed masses (kg) of white-tailed deer from Long Point National Wildlife Area, 1989 – 1994.

		Bucks				Does			
Age	Year	n	$\bar{x}$	SD	PI	n	$\bar{x}$	SD	PI
0.5	1989	48	20.0*a*	2.5	—	39	18.5*a*	3.2	—
	1990	11	25.1*b*	7.2	26	12	24.4*b*	3.4	32
	1994	5	28.8*b*	2.4	44	5	25.7*b*	4.6	39
1.5	1989	33	31.5*a*	4.2	—	33	29.4*a*	4.3	—
	1990	7	39.3*b*	3.9	25	5	36.2*ab*	6.3	23
	1994	3	61.7*c*	8.2	96	4	44.2*b*	5.6	50
2.5	1989	15	40.8*a*	7.4	—	36	34.2*a*	3.2	—
	1990	8	46.8*b*	4.6	15	6	39.1*b*	3.2	14
	1994	5	71.2*c*	7.4	75	3	50.6*c*	3.8	48
3.5	1989	14	52.3*a*	9.9	—	22	33.2*a*	3.2	—
	1990	3	64.7*ab*	18.8	24	2	40.5*ab*	4.4	22
	1994	5	74.2*b*	8.7	42	6	47.4*bc*	4.0	43
4.5	1989	7	51.4*a*	3.8	—	60	35.5*a*	4.4	—
	1990	1	59.0*	—	15	10	39.4*b*	2.5	11
	1994	0	—	—	—	2	53.0*ab*	4.2	49
5.5	1989	42	57.2*a*	9.8	—				
	1990	7	60.6*a*	5.0	6				
	1994	1	77.5*	—	36				

Note: Bucks aged 5.5 years and older are in the 5.5+ age-class and does aged 4.5 years and older are in the 4.5+ age-class. Within the same age-class, values followed by the same letter are not significantly ($P \leq 0.05$) different from one another, based on *t* tests. PI, percent increase from the 1989 mean.

* Insufficient data.

Table 2. Hind-foot lengths (cm) of white-tailed deer from Long Point National Wildlife Area, 1989 – 1994.

		Bucks			Does		
Age	Year	n	$\bar{x}$	SD	n	$\bar{x}$	SD
0.5	1989	49	41.0*a*	1.6	41	39.6*a*	1.6
	1990	11	41.0*ab*	3.5	12	41.1*b*	2.2
	1994	5	42.7*b*	1.1	3	42.9*b*	1.1
1.5	1989	31	46.5*a*	1.4	30	44.9*a*	1.6
	1990	7	48.3*b*	1.4	5	45.7*a*	1.4
	1994	3	47.9*ab*	1.7	4	44.8*a*	1.5
2.5	1989	15	48.4*a*	1.2	38	46.5*a*	1.2
	1990	8	48.8*a*	1.2	6	47.5*a*	1.0
	1994	5	51.2*b*	1.7	4	47.7*a*	1.0
3.5	1989	14	49.6*a*	2.0	20	46.4*a*	1.0
	1990	3	49.5*a*	1.8	2	46.8*a*	2.5
	1994	5	51.3*a*	1.4	6	47.0*a*	1.2
4.5	1989	6	48.9*	1.6	57	46.8*a*	1.6
	1990	1	49.0*	—	10	45.5*b*	1.6
	1994	0	—	—	2	48.7*ac*	0.5
5.5	1989	42	50.3*a*	1.4			
	1990	7	49.4*a*	1.6			
	1994	1	52.1*	—			

Note: Bucks aged 5.5 years and older are in the 5.5+ age-class and does aged 4.5 years and older are in the 4.5+ age-class. Within the same age-class, values followed by the same letter are not significantly ($P \leq 0.05$) different from one another, based on *t* tests.

* Insufficient data.

Results and discussion

Dressed weights of LPNWA deer from 1989 are among the lowest on record for the subspecies *O. v. borealis*, occurring in eastern Canada and the northeastern United States. They are comparable to those of deer in the protected and severely over-browsed Harriman State Park in New York, described as "some of the poorest specimens in physical condition ever recorded in New York and possibly the Northeast" (Dickinson 1983). Even with the substantial increases, the body masses of LPNWA fawns in 1990 are still comparable to those found on "New York's worst deer range (central Adirondacks)" (Severinghaus 1979). The mean mass of male fawns increased by 26% from 1989 to 1990 and by 44% from 1989 to 1994 (Table 1). An exceptionally small male fawn (9.5 kg) lowered the 1990 mean; without this animal the increase after 1989 would be 33%, similar to the increase of 32% for female fawns.

Yearling males showed the greatest response, with an initial increase of 25% from 1989 to 1990 and an overall increase of 96% by 1994 (Table 1). The body mass of yearling females increased by 23% in 1990 and significantly, by 50%, from 1989 to 1994. In comparison with deer harvested during the provincial controlled hunts on the adjacent wildlife management unit from 1987 to 1989, LPNWA fawns harvested in 1994 weighed less (28.8 vs. 32.5 and 25.7 vs. 30.2 kg for males and females, respectively), but in 1994, LPNWA yearlings exhibited exceptional growth, outweighing mainland yearling bucks (61.7 vs. 56.2 kg) and equivalent to yearling does (44.2 vs. 44.4 kg).

Mean mass of animals aged 2.5 years also exhibited significant ($P \leq 0.05$) increases between 1989 and 1990 and between 1990 and 1994, with an overall increase of 75% for bucks and 48% for does. Differences in density appear to affect the body mass of bucks to a greater degree than that of does. Similarly, Clutton-Brock et al. (1982) found that in red deer (*Cervus elaphus*), stag mass tends to be more responsive to differences in density than that of hinds, in which density effects are reflected to a greater degree in reproductive effort than in mass. Older animals typically exhibited a reduced but significant response when sample size was not limiting, evidence of low birth masses and poor conditions experienced during their early growth years (Schultz and Johnson 1995).

Asymptotic masses of adult bucks (5.5+) and does (4.5+) from the LPNWA 1989 hunt (Table 1) were typically 36 and 33% less, respectively, than on the adjacent mainland. By 1994, 3.5-year-old bucks and does (there were no 4.5-year-old bucks and a small sample of 4.5+ does and 5.5+ bucks) averaged 16 and 10% less, respectively, than animals on the adjacent mainland.

Skeletal growth has the highest priority among the three indices of morphology (mass, hind-foot length, and antler beam diameter) and is least affected by differences in range quality (Klein 1964). Thus, as was expected, hind-foot length showed the least response, although there were significant increases from 1989 to 1990 for male yearlings and female fawns (Table 2). In 1990, the exceptionally small male fawn decreased the mean by 9 mm, although without this animal the increase between years was still not significant. From 1989 to 1994, significant increases in length were recorded in fawns and 2.5-year-old bucks, indicating considerable improvement in the condition of maternal does and the ability of deer to forage effectively. Since almost all skeletal growth of

Table 3. Antler beam diameters (mm) of bucks from Long Point National Wildlife Area, 1989 – 1994.

	1989			1990				1994			
Age	*n*	$\bar{x}$	SD	*n*	$\bar{x}$	SD	PI	*n*	$\bar{x}$	SD	PI
1.5	27	11.2*a*	2.2	5	14.2*a*	2.8	27	3	21.6*b*	3.9	93
2.5	15	19.7*a*	3.7	9	19.4*a*	2.4	–2	5	26.6*b*	2.6	35
3.5	14	25.9*a*	4.0	3	25.8*a*	4.0	0	5	28.0*a*	1.4	8
4.5	15	29.7*a*	3.5	1	26.4*	—	–11	0	—	—	—
5.5+	41	30.9*a*	3.4	7	28.5*a*	2.8	–8	1	32.3*	—	5

Note: Within the same age-class, values followed by the same letter are not significantly ($P \leq 0.05$) different, based on *t* tests. PI, percent increase from the 1989 mean.

* Insufficient data.

white-tailed deer occurs by 2.5 years of age, these improvements suggest that LPNWA deer have not reached their genotypic potential and that the environment may still be limiting growth.

Antler growth is subordinate to maintenance and general body growth (French et al. 1956), consequently antlers tend to be more responsive to environmental stress than other morphological indices. This makes them excellent indicators of the physical condition of the herd (Severinghaus and Moen 1983; Ramussen 1985). Antler beam diameters of yearling bucks are particularly useful for assessing the condition of deer populations (Adams 1960; Ramussen 1985). Mean antler beam diameters of yearling bucks taken in 1989 ($\bar{x}$ = 11.2 mm) (Table 3) are smaller than those on record for this subspecies, indicating the extreme conditions the herd was experiencing.

Antler beam diameter and body mass are closely related (Roseberry and Klimstra 1975; Severinghaus and Moen 1983; Ramussen 1985). As LPNWA deer responded to reduced density and competition, the responses of antler beam diameter and dressed body weight were not uniform. This may be due to the relative improvement in the quality of winter and summer range in LPNWA. The body mass of deer is controlled by the history of the animal to a greater degree than is antler growth (Cheatum and Severinghaus 1950). Among other social factors, the autumn body mass of a deer is affected by feeding conditions in the previous summer, spring, and winter. Antler growth is not as affected by winter food restrictions, but depends to a greater extent upon spring and early-summer feeding conditions (Cowan and Long 1962). If feeding conditions were much better on the summer range than on the winter range before the 1989 hunt, a comparatively greater improvement in winter range conditions between the 1989 and 1990 hunts, expressed as increases in mass, may explain why initial increases in antler growth were not observed along with increases in mass. By 1994, antler beam diameters were 93% greater in yearlings and 37% greater in 2.5-year-old bucks. This was not true of older animals, as small sample sizes reduced the statistical power of our tests.

This is likely the most extreme case of white-tailed deer suppression and subsequent release ever documented. Rather than the herd being genetically smaller than other populations of *O. v. borealis*, as some had thought, these results show that the environment was limiting its genotypic potential, and illustrates the exceptional ability of the species to withstand severe environmental pressure.

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