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CHARACTERISTICS, LIBERATION AND DISPERSAL OF SIKA DEER (*CERVUS NIPPON*) IN NEW ZEALAND

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ABSTRACT

Morphological characterisation of sika deer is attempted by using a discriminant function analysis based on autopsy data from a mixed population of sika and red deer. There is evidence of hybridism between the two species. The history of liberation and dispersal from the northern Kaimanawa Mountains is illustrated by two dispersal maps based on sighting records and roar data. Spread was predominantly through shrubland or shrubland/forest ecotones. Dispersal rates varying from 0.6 to 1.5 km/yr are estimated for the period 1905-30, and then for decades to 1970, showing an acceleration after 1950 (possibly due to human activity pushing the deer westwards into indigenous forest regions).

INTRODUCTION

Sika deer (*Cervus nippon*) were liberated near Oamaru in the South Island of New Zealand in 1885 and in the Kaimanawa Mountains of the North Island in 1905. Only the second release, which was with deer from the Duke of Bedford's Woburn herd, proved successful. Since the first stalking season for sika in 1925 (McKinnon and Coughlan*, 1960) the species has been prized for its trophy value (Thornton, 1933;

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Douglas, 1952). Jordan (1931a; 1931b) considered that sika were harder to shoot than red deer; Kiddie (1957) was also of the same opinion and stressed the need to employ experienced hunters on Forest Service control operations.

By the late 1950s concern was being expressed that the preference of sika for forest browsing and the difficulty of controlling them resulted in greater potential danger to the protection forest than that represented by red deer (Elder, 1956; Schofield, 1957; Logan, 1957). A study of damage in beech protection forest in the northern Kaimanawas (McKelvey, 1957) showed that, in the areas surveyed, browsing by sika deer had inhibited all effective regeneration of beech seedlings in the canopy gaps. In addition, he suggested that occurrence of unthrifty red deer associated with sika in obviously good condition indicated that the carrying capacity, lowered by red deer to their own detriment, was still sufficiently high to support a considerable sika herd (McKelvey, 1959). This is taken to imply that browsing by sika could degrade the forest beyond the level of damage caused by red deer.

During 1963-66 the New Zealand Forest Service investigated the factors underlying the dispersal of sika deer from their point of introduction southwards along the Kaweka Range to the Ruahine Range. Observations were made in the Oamaru Valley, Kaimanawa-Kaweka, on the pattern of habitat occupation and use by a mixed population of sika and red deer. As it was believed that hybridism takes place between sika and red deer, information was obtained from overseas about the characters of the stock from which the sika in New Zealand originated, and autopsies were carried out to determine the morphological characteristics of both the sika and red deer species in the Kaimanawa-Kaweka region. Herd structure, reproductive success, and behaviour were also studied. Fig. 1 shows the area of the North Island now occupied by sika deer.

TYPE ORIGIN

The type origin of sika deer in New Zealand is a matter of some dispute. Donne (1924) states that the Duke of Bedford identified the sika which he gave to New Zealand as the Manchurian type, but other writers (Lydekker, 1901; Bedford, 1949; Whitehead, 1950, 1964) record that there were five subspecies of sika deer at Woburn Abbey at the turn of the century. Glover (1956) describes the mixing of races of sika before their entry into Britain, and considers that the sika sent to New Zealand were of very mixed origin.

From observations made in the Kaimanawa-Kaweka area during the course of the sika deer research project, there appears to be little doubt that sika deer in New Zealand are indeed of very mixed origin. For this reason they are classified simply as *Cervus nippon.*

DEFINITION OF SIKA DEER

Differentiation from Red Deer

Observations were made on a group of deer in the Oamaru Valley, the boundary between the northern Kaimanawa Mountains and the Kaweka Range. Numbers of these deer varied with the season, from nil on a day in June 1964 to a maximum of 140 in November 1966. Two species of deer were expected in the area; the descendants of sika deer which had been liberated in the northern Kaimanawas in January 1905, and red deer which had infiltrated from distant liberations.

STUDIES OF THE SIKA DEER IN NEW ZEALAND

(Mavis M. Davidson)

Locality Map

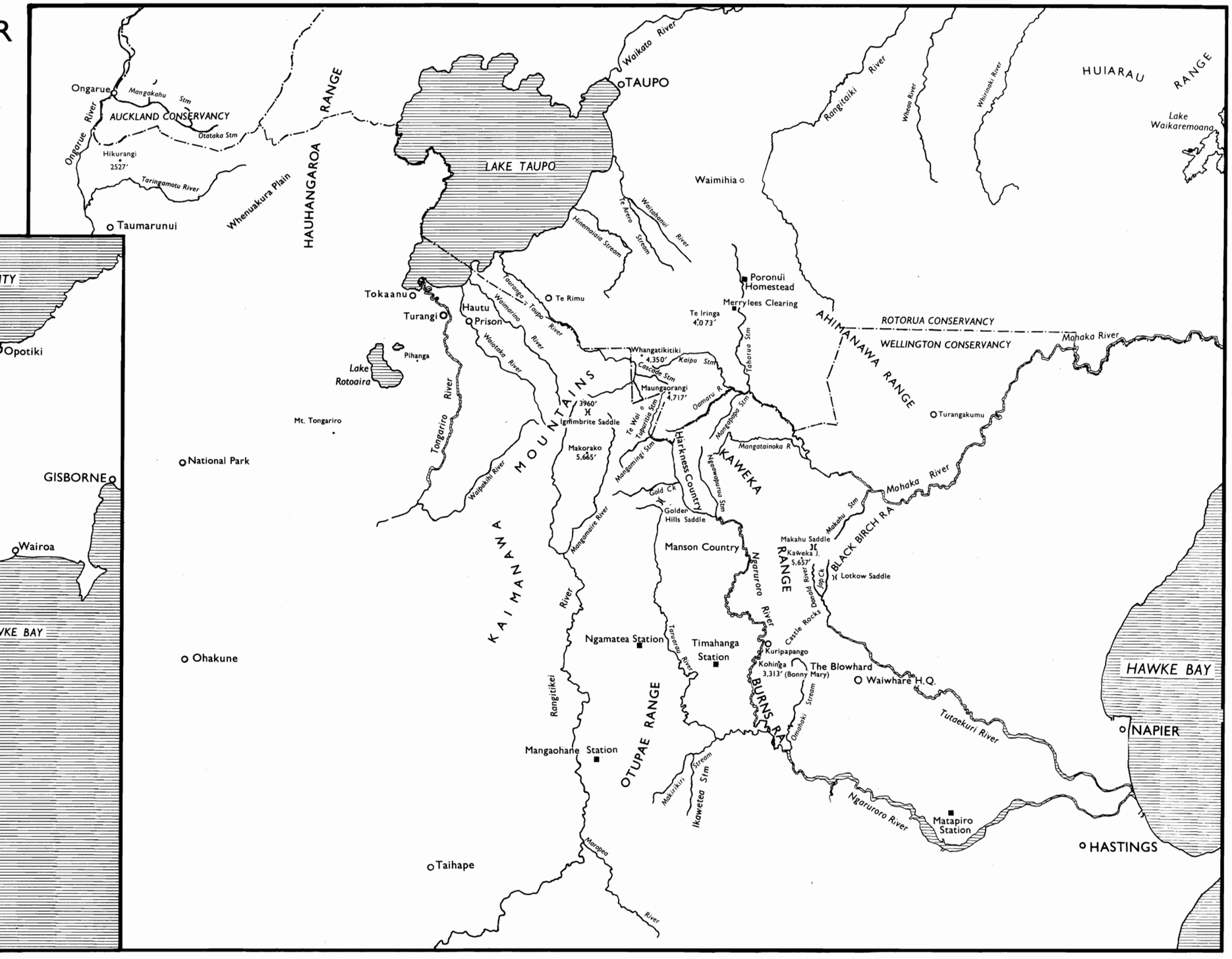

FIG. 1—Map of central North Island showing area of occurrence of sika deer.

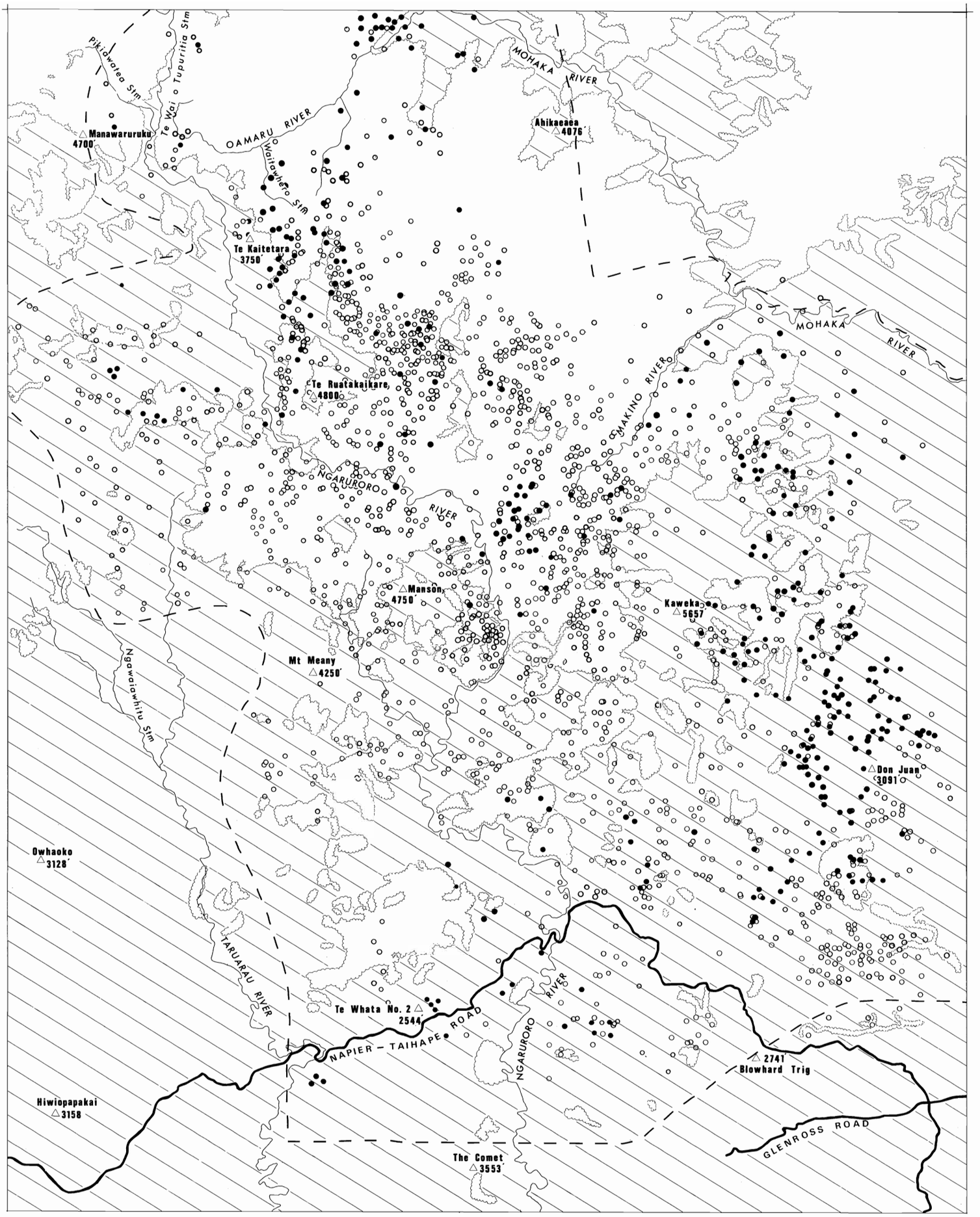

FIG. 14—Dispersal of sika deer through Kaweka Range determined by plotting stag roars. A preference for the shrub- and tussock-lands in autumn is indicated.

● Sika deer ○ Red deer

Age groups (i.e., fawn, yearling, and adult) and sex could be distinguished, except in the case of young fawns. By the end of the fawn year, however, sex could be determined because incipient antler pedicles had become apparent in the males, and their behaviour was different from that of female fawns.

Deer were shot and autopsied in areas adjacent to the Oamaru Valley during the period 1963-66 to determine whether there were characters distinguishing the two species. These deer were described by the hunters as "sika", "red", or "suspected hybrid", on the basis of general appearance and pelage. One hundred and sixty-seven (98 female and 69 male) sets of measurements were taken from the carcasses of adult animals. Tail length, head length, ear length, rear foot length, hoof tip to metatarsal gland length, height at shoulder, chest girth, and body length, were then used in a discriminant function analysis (Cooley and Lohnes, 1971) for deer of over 36 months, and for which complete records were available (60 females and 47 males). Ages were verified by study of the dental cementum layers (Douglas, 1970).

Discriminant scores for data for adult males generally fall into two groups, i.e., a range of 1.9 to 2.4 for sika deer and 2.6 to 3.0 for red deer (Fig. 2). For adult females a similar pattern emerges, the discriminant scores showing a range of —1.8 to —2.2 for sika, and —2.3 to —2.7 for red deer (Fig. 3). Differentiation of sika and red deer is clearly shown by Rao's F test for significance of the eigen values: for male adults, the F ratio is 35.94, with DF 1 8 and DF 2 60, and the normal deviate 8.87; for female adults the F ratio is 47.66, DF 1 8 and DF 2 90, the normal deviate 10.77 and in each case the probability is 0.0. In general, field identifications assigned the deer to the correct species. In the analysis only eight (3 male, 5 female) identifications fell below a probability of 95%. Four of these deer (1 male, 3 female) showed intermediate characters and it is likely that they are hybrids. In the field two of these were identified as hybrid females (shown as queries in Fig. 3). The averages of characters for animals identified as adult sikas by the analysis are given in Table 1.

TABLE 1—Characterisation of sika deer from discriminant function analysis: Means of selected characters of not less than 95% probability and discriminant values.

	Sika males (N = 47)		Discriminant value	Sika females (N = 60)		Discriminant value
	$\bar{x}$ (mm)	s.d. (mm)		$\bar{x}$ (mm)	s.d. (mm)	
Tail length	128	16.3	—0.5513	112	19.8	+0.2716
Head length*	326	20.5	+0.3033	295	18.3	—0.2342
Ear length	136	7.0	+0.6425	128	6.2	—0.6141
Rear foot length	415	17.2	+0.3743	391	13.6	—0.3367
Hoof/metatarsal length	306	16.3	+0.1670	286	12.2	—0.0196
Height at shoulder	892	48.5	—0.0935	817	42.0	—0.1206
Chest girth	919	55.5	+0.0822	822	48.0	—0.0725
Body length	1398	84.7	—0.2383	1313	66.0	+0.0805

* Over the pelt

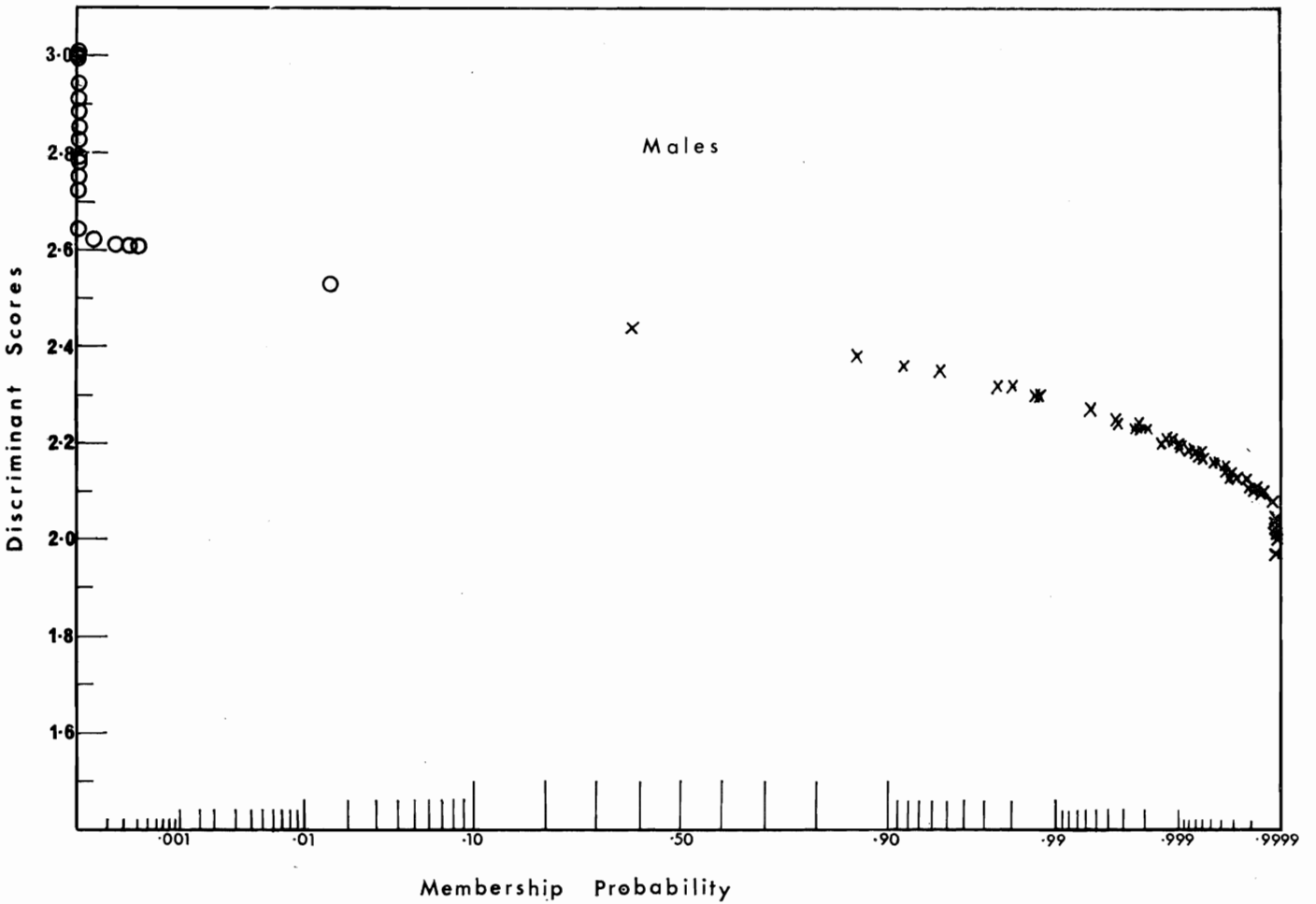

FIG. 2—Discriminant function analysis of mixed sika-red deer populations. The figure shows discriminant scores derived from eight variables plotted against the probability of membership of the observations to sika and red deer groups (males). Observations with probabilities greater than 0.9999 are represented on the ordinates for this value at the side of the figure. Key: O = red deer, X = sika deer.

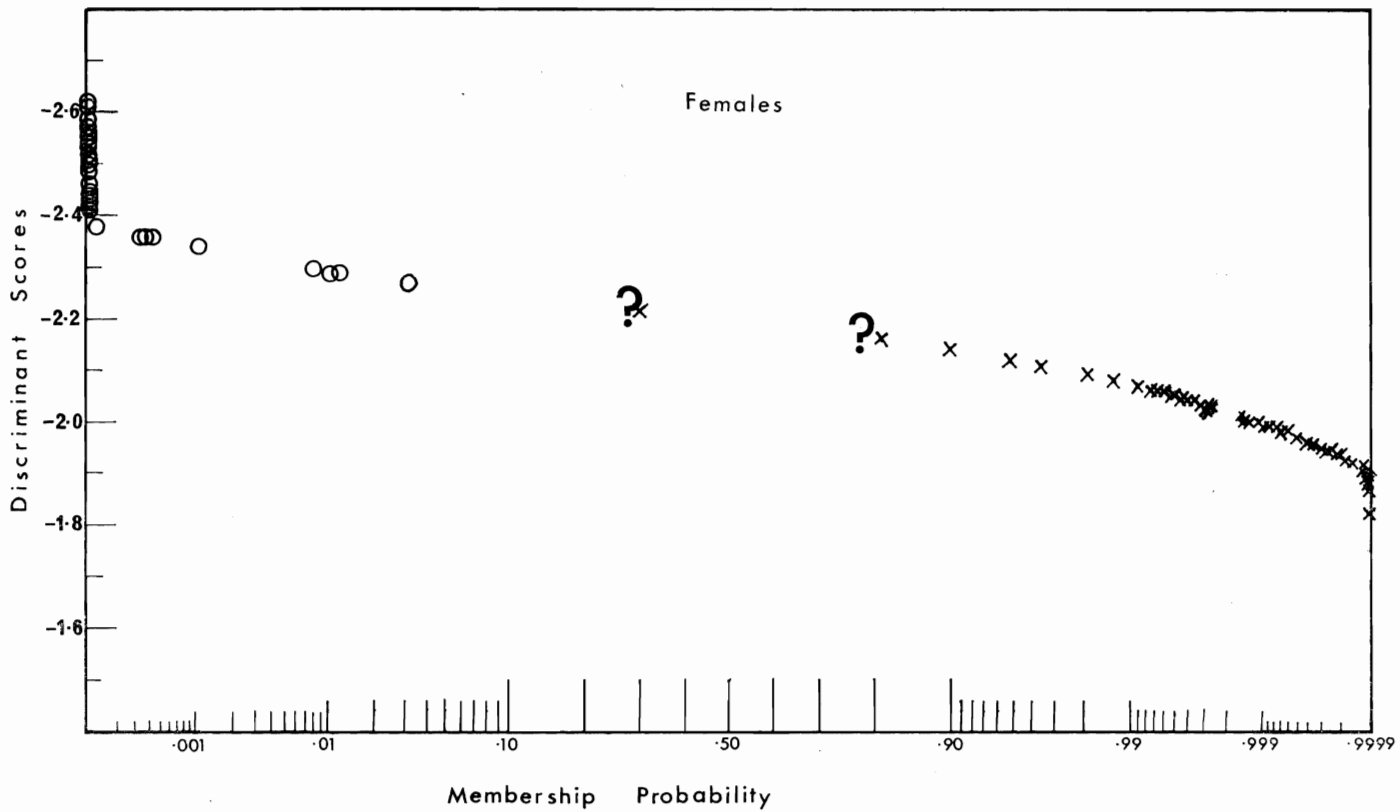

FIG. 3—Discriminant function analysis of mixed sika-red deer population: female. Key: O = red deer, X = sika, ? — identified as hybrid in field.

External Characteristics

Pelage

Winter coat.

From a distance, or when wet with rain, the overhair (Searle, 1968) of the winter coat of sika deer appears to be uniformly black, but at closer range it usually looks brownish-black with faint spots. The crinkled, closely set individual hairs are pale grey almost to the distal end, where there is a short length of black and a final tip of gold, giving the brownish-black surface colour.

Close to the pelt very fine, white, gossamer-like underhair forms an insulating mat, or "wool" (Kiddie, 1962; Holden, 1969). Towards the belly the black pigment fades out and the hairs are gold-tipped grey, shading into the darker grey-brown of the legs. Anteriorly, the white belly hair is tipped with grey, more heavily in the male. Posteriorly, the belly hair is sparse and white, except that in the male it may be stained blackish during the roar. A black dorsal stripe extends from the head to the tail but is not so well defined as in the summer coat. With the winter coat the sika stag grows a thick mane, the hairs appearing brownish black for most of their length, and pale brown for the last 30 mm or so. Hinds and young sika have a slightly paler coat than the stag, and at a distance may look grey. The winter coat of the sika is much thicker and heavier than that grown in summer.

Summer coat

The overhair of the summer coat of the sika is a sleek bright chestnut conspicuously dappled with white (Figs. 4 and 5); the under-hair is not readily identifiable. The

FIG. 4—Sika stag in summer pelage, with developing antlers (Dec., 1966). (Photo: Mavis M. Davidson.)

FIG. 5—Sika hind nearly into summer coat (Nov., 1966). Note white hair of rump patch, chin, ears, "Y" chevron. (Photo: J. H. Johns.)

overhair, which is sparsely set, becomes paler and unspotted towards the belly and down the legs, which are grey-brown; the belly hair is white, becoming very sparse anteriorly. In general, stags are not spotted or only lightly so along the centre of the back, the spots being small. However, some males have very large spots which are continued right to the backbone resembling those in a photograph used by the Duke of Bedford to illustrate the large Pekin sika (Bedford, 1949). Although, as Bromley (1956) points out, there is considerable variation in pelage colour even in an isolated population, these different spotting patterns tend to confirm a hybrid origin for the sika in New Zealand (Glover, 1956).

The black dorsal stripe runs from the back of the head to near the base of the tail, where it enlarges to a black patch interspersed with chestnut hair similar to the main coat. Many sika have some white hairs on the throat but a distinctive white throat patch (not as conspicuous as that in Fig. 6) was recorded for only seven sika in this study.

The head

From the nose or muzzle of the sika in the usual winter pelage, short, fine, glossy brown hair, tipped with gold, extends to a point between the eyes, the fine hair continuing in a curve to the posterior margin of the eyes. The edge of the fine hair shows up as a shallow "Y" against longer, coarser hair growing in front of and between the pedicles bearing the antlers in the stag, and the equivalent position in the hind. A band of pale brown hair above the eyes has the appearance of an eyebrow; this continues as a slender line around the eye and accentuates the preorbital gland. Above and below the eye some 20 to 25 stiff vibrissae reach a length of about 50 mm.

In summer the hair on the head of the sika is a paler extension of the bright coat,

FIG. 6—Sika stag with white throat patch, shot by J. Dobson. (Photo: N. Douglas.)

but where the fine hair finishes there is a distinct band of off-white (Fig. 4) across the frontal bones, reminiscent of the "chevron" described by Grimwood (1964) for the hirola or Hunter's antelope (*Damaliscus hunteri*). This band is confluent with the paler hair which encircles the eyes, and which is more pronounced in the summer pelage.

On the nose of the sika there is a patch of off-white hair on each side of the rhinarium. The white patches narrow posteriorly and extend along the upper lips. Two larger, oval patches of off-white hair continue posteriorly from the chin (*see* Fig. 5). Stiff, black vibrissae up to 70 mm emerge sparsely from the overhair on the nose and beneath the chin, and softer, finer hairs from 10 mm to 20 mm occur on the rhinarium. Posterior to the chin patches, pale brown hair extends down the throat to the shaggy two-toned mane of the winter coat in the male; in summer the pale brown tone is more uniform.

The medial edges of the nostrils in sika tend to be rounded whereas those of red deer are more V-shaped; there is also a difference in aerolation of the rhinaria of the two species.

Rump patch

The rump patch is thought by Lydekker (1901) to be the best distinguishing character for sika. In New Zealand it appears as two round, black-margined areas of coarse, crinkled white hair, divided by the central black stripe on the long white tail; it is retained throughout the year but is less conspicuous in winter. According to Ahlen (1965) some of the red deer in Norway and Sweden also have a black margin to the

rump patch, but this is not known to the writer for red deer in the Kaimanawa/Kaweka area. However, both the Thorndon strain of red deer in the Nelson district and Warnham deer in Dusky Sound, Fiordland, usually have a black margin to the rump patch (C. L. Batcheler, pers. comm.).

The area of the sika rump patch is not as extensive as that of the red deer, but the hairs are erectile and may be flared in semblance of a fan when the deer is alarmed or disturbed in some way; so that the sika rump patch can attain a prominence unmatched by that of the red deer, the hairs of which are weakly or non-erectile.

Although the most readily distinguishable single feature of sika is the white rump patch, some variation was observed during this study. Colour of the rump patch ranged from white to dark cream, and in some cases the black margin was missing. Sowerby (1929) records eastern Asiatic sika deer with "croup-disc white to cream-white or buff".

The new-born fawn has a light brown rump patch (as also are the hairs of the metatarsal tuft) for some two to three months, and in the case of one sika fawn it remained brown for nearly a year. The coat of the sika fawn is similar to the summer coat of the adult but the markings may not be so well defined. Spots are lost at about four months of age.

The ears

The ears of sika deer are shorter and more rounded than are those of red deer (Fig. 7). In summer, the white hair inside the sika ear is sparse, and dark blotches may

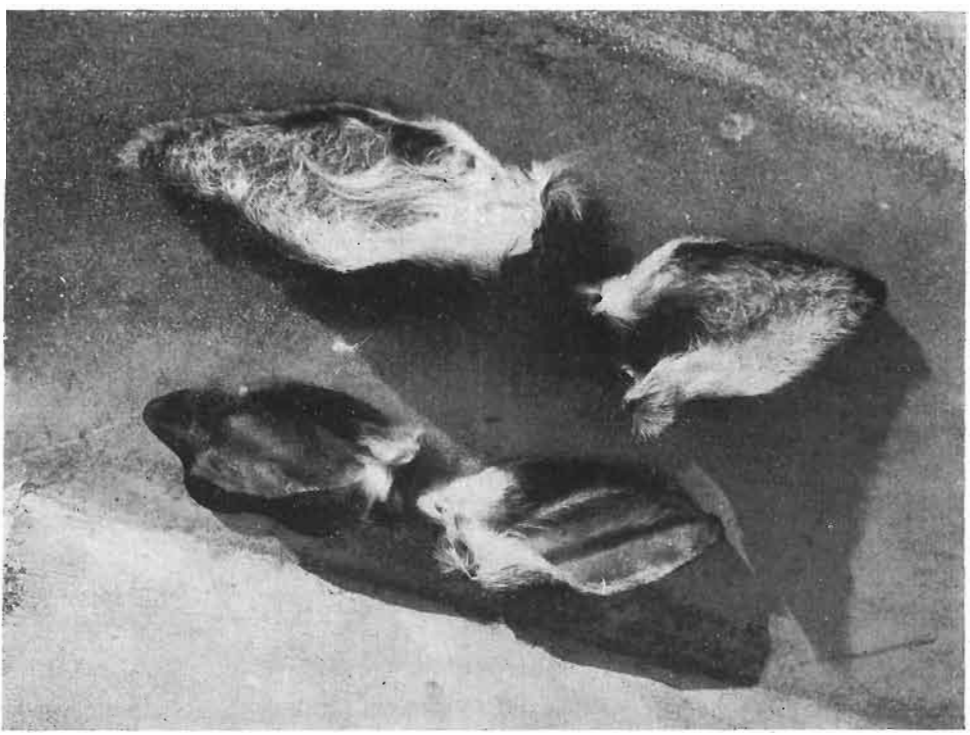

FIG. 7—Top: ears of red (left) and sika deer in winter. Lower: ears of sika deer in summer. (Photo: Mavis M. Davidson.)

be seen on the skin beneath, or in some instances a black margin as found bordering the ear of red deer can be present. In the winter, the white hair becomes very thick, even matted. Hair on the outside of sika ears is similar to the seasonal coat, and at all seasons the white hair of the inside is very conspicuous when the deer is alerted.

The tail

Lydekker (1901) notes that in sika the tail is much longer than in the red deer group. Hair lengths of up to 330 mm have been measured in New Zealand for sika.

In sika deer the tail is white, the tip curling upward and outward. There is usually a central black stripe, but this may be absent or represented only by one or two black spots. In contrast, the hair colour of the tail in red deer is similar to the rump patch, and extends comparatively little beyond the distal vertebra.

Metatarsal tuft

The metatarsal tuft of hair surrounds the metatarsal gland, a patch of modified skin situated on the metatarsus (cannon bone) in certain Cervidae. Its position has been used by Gray (1836, 1872), Caton (1877), and Brooke (1878) as a criterion for division of the Cervidae.

In sika deer in New Zealand a prominent metatarsal tuft occurs on the postero-lateral surface of the metatarsus, a short distance below the tarso-metatarsal joint. The tuft is variable in shape and colour (Figs. 8 and 9) but is chiefly oval, the ventral hair tapering

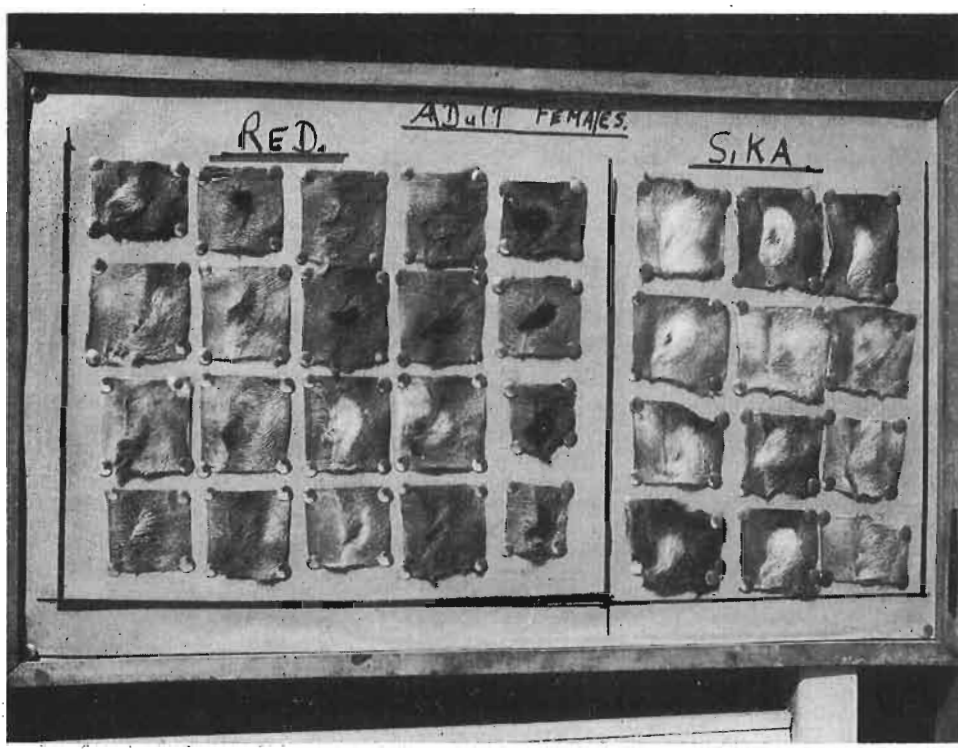

FIG. 8—Metatarsal tufts of adult sika and red deer: females. (Photo: Mavis M. Davidson.)

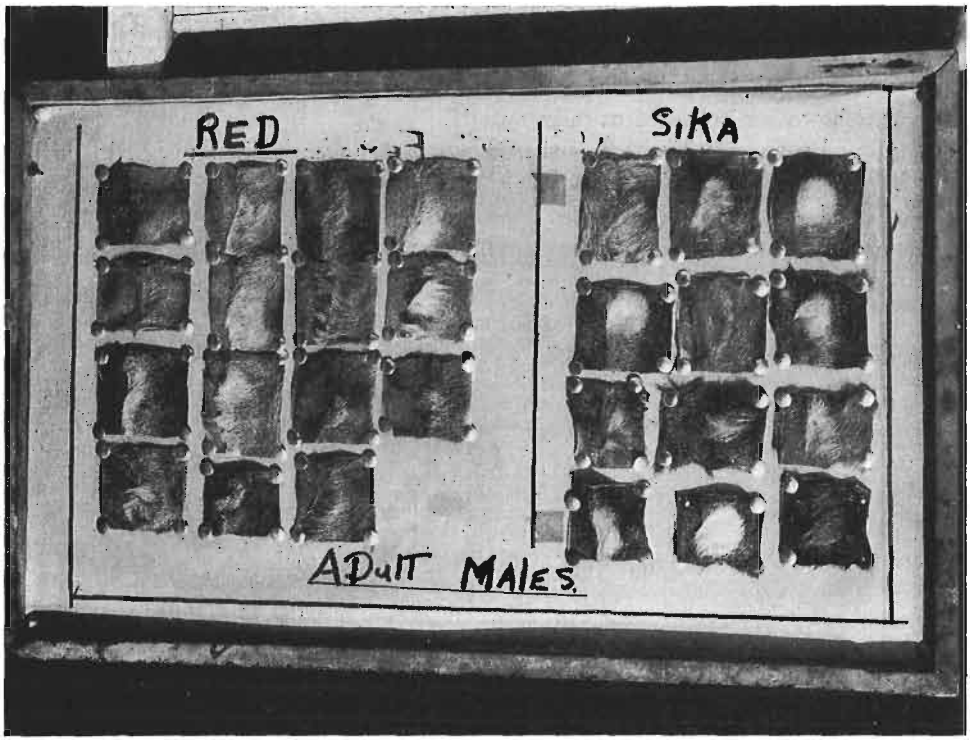

FIG. 9—Metatarsal tufts of adult sika and red deer: males. (Photo: Mavis M. Davidson.)

and sweeping anteriorly. The colour varies from whitish through various shades of cream and brown to tan, and may be little different from the colour of the leg hair in the summer coat; in general it shows up as a very conspicuous pale patch. Of 54 females defined as sikas at the 95% probability level in the analysis, 45 had light and 9 dark metatarsal tufts, and of 42 males, 30 had light and 12 dark tufts.

In red deer the metatarsal tuft tends to be less conspicuous, a notable exception being that of red deer hinds from the Tauranga-Taupo headwaters, northern Kaimanawas, which had very distinct dark-brown or black metatarsal tufts (Fig. 8). An occasional red deer had a light beige tuft.

Coat change

Prevailing weather conditions appear to have a bearing on moulting, but there are few quantitative data. Hershkovitz (1958) records that moulting in neotropical forms of white-tailed deer (*Odocoileus virginianus*) is a continuing process without notable change in pelage type. With sika, moult from the summer to the winter coat takes place so slowly that it can simultaneously show the summer and winter coat; this transitional stage is called the "autumn coat" by Dobroruka (1960).

Fig. 10 shows autopsy records of coat condition of adult sika deer. Overlapping summer, winter, and moulting conditions suggest that sika deer in New Zealand have a transitional "autumn coat", and also a "spring coat". Full winter and summer coats are shown for only two to three months.

Stags and young sika observed in the Oamaru Valley are usually out of their summer coat by the roar, but the hinds tend to carry the autumn coat longer, and it can be the end of May before the winter coat appears. In November, or even earlier, some sika have summer coats but it is not general until well into December and can be much later.

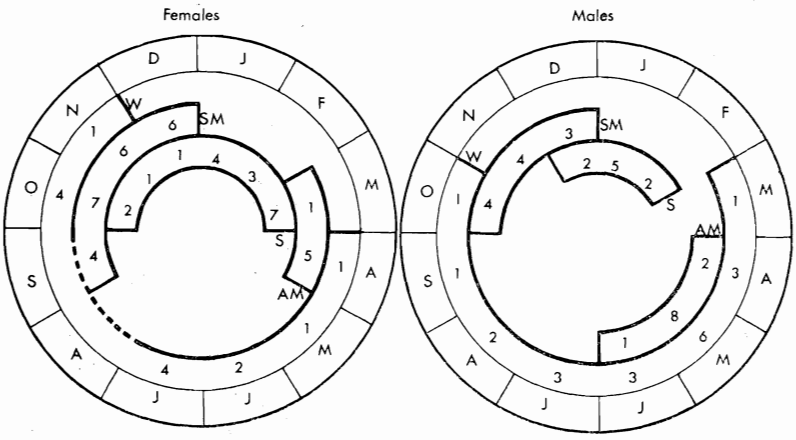

FIG. 10—Coat changes in adult sika
Key: Outer circle — calendar months
W = Winter coat
SM = Summer moult
AM = Autumn moult
Inner circle S = Summer coat

Antlers

Antler form

Douglas (1959) has described the antler form of all the deer species in New Zealand, and his illustrations show that sika antlers resemble those of red deer except that the sika has no bay tine; this condition also occurs in some red deer (Thomson, 1952). Notable sika heads in New Zealand have been recorded by Thornton (1933), Douglas (1952), East (1954), and by *New Zealand Wildlife.*

Kiddie (1962) distinguishes sika antlers as giving off the brow tine some distance above the burr, and those of red deer close to the burr, but this distinction is not constant. Observations in the Oamaru Valley indicate that the age of a sika deer, as verified by counts of dental cementum layers (Douglas, 1970), cannot be told from the number of antler points. An immature sika in its third year (30 months) had eight points, while many adult stags had only two spikes.

Antler velvet colour

Sika antler velvet has been described by various writers, and at least two subspecies of sika are distinguished by this feature: Manchurian (tan-reddish, with some black on tines) and Japanese (grey or black). Other variations have been noted (Bromley, 1956;

Goss, 1967; and for New Zealand, Douglas, 1959; Kiddie, 1962 and Holden, 1969).

In the Oamaru Valley, the highest recorded tally of antler colour for any one observation period was 12 sika stags with purplish-black velvet, and six with a rich reddish velvet, which appeared translucent in the earlier stages. No black markings were noted.

Antler shedding and regrowth

Antler change occurring in male deer autopsied in the Kaimanawa/Kaweka area is illustrated for sika and red adults, sika third-year animals, and yearlings (Fig. 11).

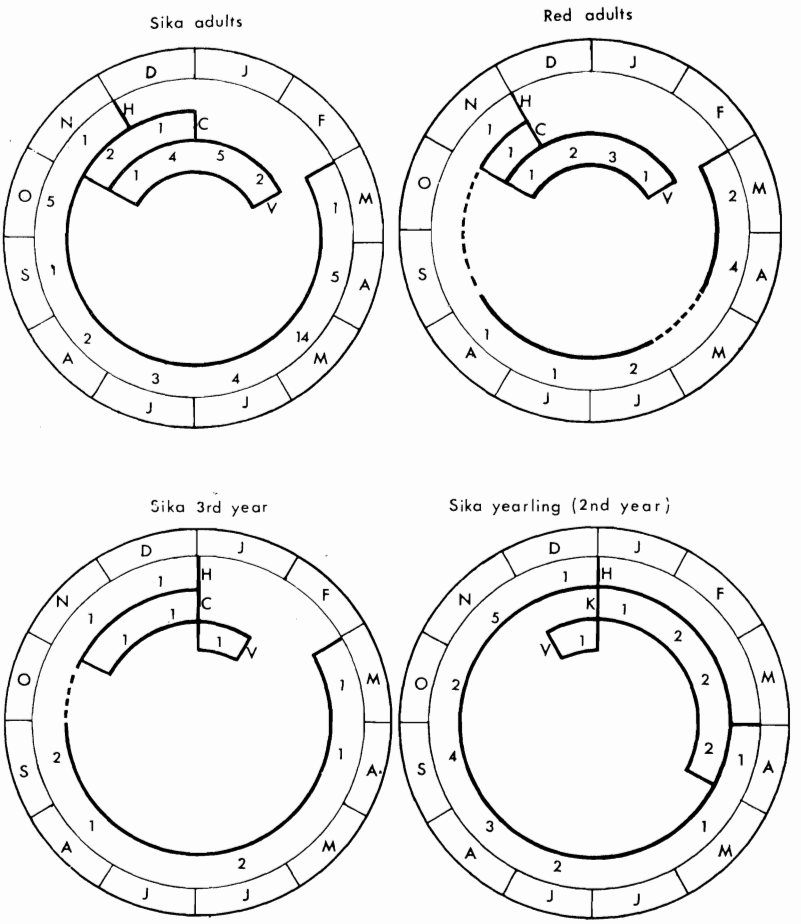

FIG. 11—Antler change in sika and red deer adults, sika third year and yearlings

Key: Outer circle — calendar months

	Ages:	
H = hard	Fawns	0-12 months
C = cast	Yearlings	13-24 months
V = velvet	3rd year	25-36 months
	Adults	> 36 months

Data from this small sample show similar times of change for sika and red adults in this region, with antlers in the hardened state from March to November, in velvet from November to February, and with casting commencing in November and continuing into December for sika. The sample of red adults, however, is too small for results to be conclusive. In Cupola Basin, Travers Valley, red deer cast their antlers earlier than this (C. L. Batcheler, pers. comm.). Third-year sika males retain hardened antlers from March until December. Two third-year animals show a casting pattern similar to the older sika (*see* Fig. 11). These two deer, however, were aged as 36 and 36 ± 2 months and so were virtually adult. Likewise, the yearling sika show antlers still hard in December, the one example of a deer in velvet being a spiker of approximately 24 months of age.

The same age-specific pattern was recorded for antler casting. Generally speaking, sika adults appear to cast their antlers in November-December; yearling and third-year sika cast in December-January. Isolated records of casting outside the period have been known. During the present study some of the younger males did not cast their antlers until January, or even February. By mid-March most of the older stags (both sika and red deer) have hard antlers with white tips or with shreds of velvet hanging from the antler tips, though there might still be a few big "racks" in velvet, as well as those of younger sika males. In general, results from the Kaimanawa/Kaweka area indicate that the whole cycle of antler shedding and regrowth is similar in sika and red deer, as reported by McNally (1968) for Scotland, by Pocock (1912) and by Harris and Duff (1969) for England, and by Hollister (1920) for zoological park deer in America.

LIBERATION AND DISPERSAL OF SIKA DEER

It is generally thought that the first sika deer in the North Island of New Zealand were released in a clearing (now known as Merrylees) on the eastern side of the northern Kaimanawa forest (State Forest 90), between the upper and lower homesteads of the Taharua (now Poronui) Station.

Thomson (1922) and Wodzicki (1950) record that six sika were liberated, as do McKinnon and Coughlan (1960) in their compilation of extracts from the annual reports of the Department of Tourist and Health Resorts for 1907, 1908, and 1909. Subsequently, however, Lanna Brown (pers. comm.) has drawn attention to a Department of Tourist and Health Resorts summary of game imported into New Zeaalnd for 1900-1907, in which it is stated that three females and one male were liberated, two stags being killed at the time of release.

HABITAT AND BEHAVIOUR

Sika deer are concentrated in the Kaimanawa Mountains (principally the northen Kaimanawas), the Kaweka and Ahimanawa Ranges. They have also penetrated the forests of the southern Urewera, north-west Ruahine, and those of West Taupo. The dominant forest types inhabitated by sika in this area are red beech with kamahi and shrub hardwoods; red and silver beech with kamahi; mountain and red beech; and black, silver and red beech with shrub hardwoods (K3, K6, K7 and K9 respectively in the classification of McKelvey and Nicholls (1957)). In a winter survey Logan (1957) found that mixed red and silver beech (K6) was the most favoured association. Detailed

descriptions of the vegetation can also be found in Elder (1948, 1959, 1962, 1965), Poole (1950), Druce (1952), and McKelvey (1963).

Burning, and grazing by sheep, in the last century has reduced the vegetative cover, exposing the underlying pumice soils (Baumgart, 1952, 1954) to erosion. This is particularly severe in the eastern Kaweka (McKelvey, 1959). Superimposed on this pattern is the effect of introduced wild mammals, which have further depleted the forests, changing the composition and density of both understorey and ground cover, particularly along streambeds.

Sika deer were released at the edge of silver beech/red beech forest where they have established successfully. Kill data show that for most of the year sika inhabit the adjacent forest/shrubland ecotone and low-level shrub and tussock lands, moving up into the beech forest for the winter (*see* Fig. 12).

By autumn the tussock flats and shrublands in the Oamaru Valley appear to become unfavourable to sika deer, probably because of low winter temperatures and heavy frosts. A temperature of —15°C was recorded in August, 1966 (Davidson and Gannaway, 1967). Similarly, Cunningham (1964) found that in the higher, eastern Kaweka, manuka

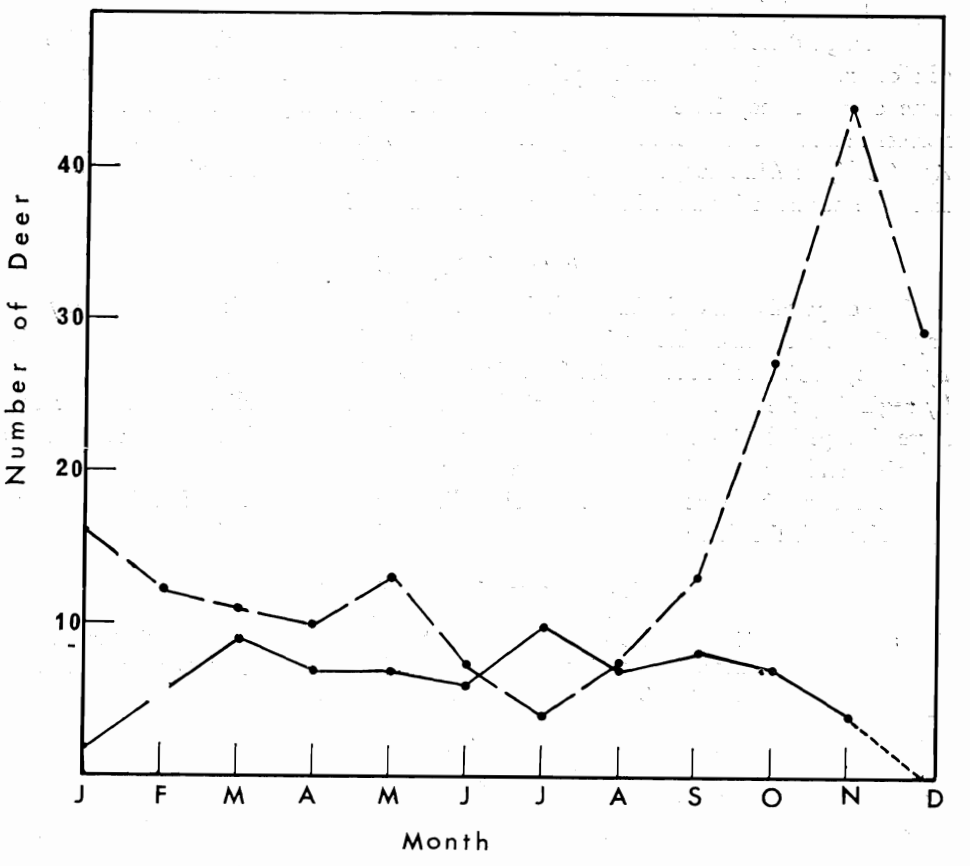

FIG. 12—Seasonal movement of sika deer derived from kill figures.
——— UF = upper forest
* — — * LF = lower forest/shrubland ecotone and low level tussock grasslands

shrubland experienced the greatest extremes of temperature and was much colder than forest in winter.

Sika return to the lower forest/shrubland ecotone in spring, utilising adjacent tussock land from before dusk until after dawn, daylight use of these open areas depending upon hunting pressure.

GENERAL DISPERSAL

In 1957, Logan reported that sika deer could be found throughout an area covering 10,500 km^2. Kiddie (1962) considered them to occur over some 11,370 km^2, i.e., from about 37° 30′ (Te Aroha) to 40° S (Tikokino), and from about 175° 45′ (Mt Pihanga) to 176° 45′ E (Urewera).

Kiddie (1962) gives Mt Pihanga as the most western point for sika range, but recent reports have extended the boundary much further westwards.

From records available to the author, sika have now been sighted 172 km north, 125 km west, 185 km south, and 60 km east of the 1905 liberation point. Sightings and their sources can be found incorporated in Appendix II. These are used to compile a dispersal map (Fig. 13).

Although these farthest-known sightings have been treated as the result of dispersal of sika from the 1905 liberation point, the possibility cannot be ruled out that in fact some of them may have resulted from illegal transplanting of this deer. The most northern and most southern sightings, Elliott (1953) at Te Aroha and *Wairarapa Times Age* (1964) at Alfredton, respectively, are the most likely to come within this category and have not been included in Fig. 13; they are noted in Fig. 1.

Rates of Dispersal

The dispersals rates of sika are difficult to determine because it is only recently that any other than casual observations have been made. Table 2 shows the area occupied by sika by 1930 and in the decades following, up to 1970. Dispersal rates were calculated by regarding the area occupied as a circle and measuring its radial extension for each successive period. Rates are shown for first sightings (either lone stags or breeding colonies) and for established breeding colonies.

No records have been found for sika dispersal between liberation in 1905 and 1930 although the first stalking season was opened in 1925 (McKinnon and Coughlan,

TABLE 2—Dispersal of sika deer 1905-70

Years	Number of Sightings		First sightings		Breeding colonies	
	Lone Stags	Breeding Colonies	Area/Year (km^2)	Rate/Year (km)	Area/Year (km^2)	Rate/Year (km)
1905-30	0	2	803	0.6	803	0.6
1931-40	2	4	2512	1.2	1917	0.9
1941-50	2	2	4273	0.9	3186	0.7
1951-60	3	12	10412	1.1	6915	1.5
1961-70	9	7	20202	2.1	11836	1.4

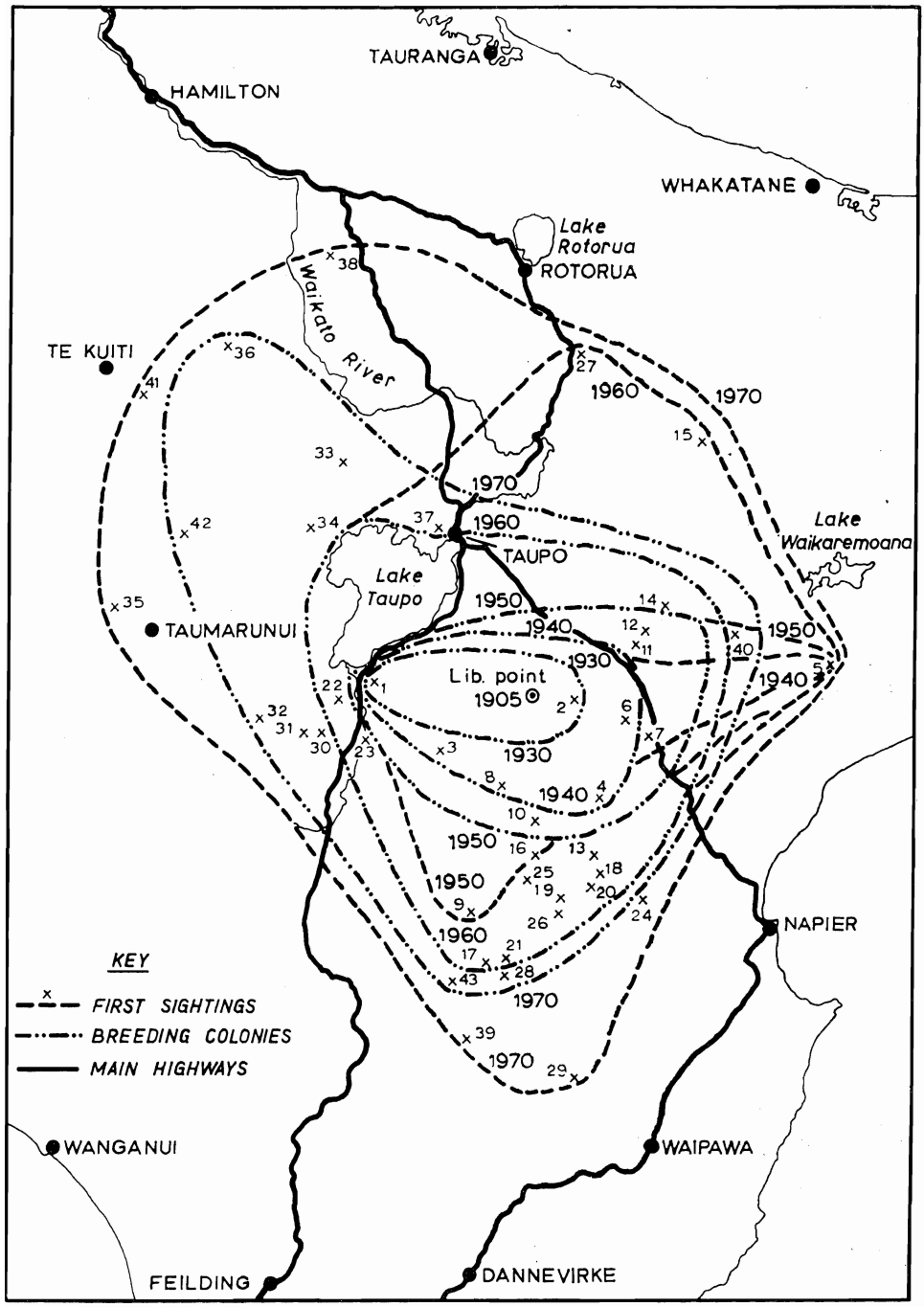

FIG. 13—Dispersal of sika deer from recorded sightings 1905-70.

1960), implying a substantial buildup of the sika herd. The rate of 0.6 km for this period is therefore likely to be minimal. The lack of records for sightings of lone stags obscures the picture assuming that the males occupy the vanguard of dispersal as Caughley (1970) found for thar.

After 1925, many good heads were taken by trophy hunters (Thornton, 1933) and sika were also encountered during Government control operations on red deer. By 1940 knowledge of sika was increasing, and the annual dispersal rate works out at 1.2 km for first sightings and 0.9 km for breeding colonies. Except for the 1951-60 decade dispersal rates of first sightings were greater than those for breeding colonies. For this period the rate for breeding colonies was calculated as 1.5 km compared with the first sightings rate of 1.1 km. In addition, there were far more sightings of breeding colonies than of lone stags (Table 2).

For the years 1951-70 there is an apparent acceleration of dispersal compared with the previous 45 years. Many factors could be involved: effect of hunting; more rapid movement through forest already depleted by red deer; the impact of logging and farm development operations; a growing knowledge of the existence and characteristics of sika deer; paucity of early records, or a changing combination of these factors.

Dispersal Routes

It is considered that the main dispersal routes of sika deer have been through shrublands, or shrubland/red beech forest ecotones. The greatest dispersal has been to the north-west, initial movement being westwards through the bush saddles into the headwaters of the streams flowing into Lake Taupo, and so into the shrublands which encircle the lake. Before the recent development of Taupo and Turangi there was a continuous shrubland route past each end of the lake.

Another dispersal route (Figs. 13, 14 see fold-out) involved direct access through the shrublands which extend down the Mohaka Valley between the Ahimanawa and the Kaweka Ranges, along the forest edge of the eastern Kaweka, and south to the Burns Range outlier, in the "corridor" between the Kaweka and the Ruahine.

A route also followed shrublands to the margin of the Urewera forest (Fig. 13), on the east of the developing Kaingaroa exotic forests, which have not become preferred sika habitat. A further route followed the Ngaruroro Valley, spreading through low saddles of the upper Oamaru, or from splinter movements from the main north-west dispersal. The Ngaruroro route splits in the Golden Hills area, with dispersal down the Ngaruroro and Taruarau Valleys. Logan (1957) implies that the founders of the sika colony living in the red beech forest of the Makirikiri area, north-west Ruahine, dispersed there by way of the eastern Kaweka. He mentions, however, that a more direct route would have been through the head of the Oamaru River to the edge of mountain beech forest extending down the Ngaruroro River, thence to the Ikawatea Valley. The writer favours dispersal through the Oamaru Catchment because at that time sika had been reported only midway along the eastern Kaweka (M. Robson, pers. comm.), and suggests that dispersal was not down the Ngaruroro Valley but by way of the easier Golden Hills saddle, thence through the Taruarau Valley and Otupae country. In 1952, there were two main colonies of sika in the eastern Kaweka, located in the Makahu and Lotkow areas of the Black Birch Range (M. Robson, pers. comm.). By

1962 sika were known to be in seven areas, the farthest being some 15 km south-west of Lotkow Saddle. Having reached the southern end of the Kaweka the deer were fanning out, moving towards the south-east, due south, and to the south-west, into the "corridor" between the Kaweka and Ruahine Ranges.

The major tussock grasslands of the Ngamatea plateau, which lack cover and have been occupied by sheep since last century, appear to have impeded direct dispersal of sika deer south and south-westwards. Similarly, the exotic forests of the north-east have probably hindered movement in that direction.

ROAR DATA

Comprehensive roar surveys for the years 1962 to 1965 were organised by M. Robson to show the distribution of sika and red deer in the Kaweka Range. The roars of sika and red deer are easily distinguished—whereas the red deer has a single bellow, the sika has a shrill whistle/scream which rises to a peak, falls and rises again several times. Forest Service rangers and Government hunters were required to plot on maps where roars were heard. The results show small groups of sika within a much greater population of red deer (Fig. 14).

Roars plotted were combined to arrive at the proportions of sika and red deer in the years 1962-63 and 1964-65 (Table 3). Sixteen and a half per cent of the roars heard over this period were sika, 83.5% were classified as red deer. The data also suggested that the proportion of sika increased significantly over the four years, from 13.3% to 19.6% ($P < .001$).

TABLE 3—Roars of sika and red deer stags, Kaweka Range

	Sika	Red	Total
1962-63	138	897	1,035
1964-65	177	723	900
	315	1,620	1,935

Fig. 14 also indicates the sikas' preference for shrublands, mainly manuka (*Leptospermum scoparium*), in the eastern Kaweka. M. Robson (pers. comm.), however, reported that in August and September 1962 there appeared to be a more even distribution of sika over the whole area. Similarly, L. Hampson-Tindale (pers. comm.) noted that in 1968 sika were localised in the autumn, but that in the winter they were more widely dispersed.

Control operation data

The records of animals killed from 1959-71 in three Kaweka hunting blocks, (1) Tutaekuri, (2) Mohaka, and (3) Ngaruroro (*see* Fig. 1), are given in Table 4. Over all, sika made up 17% of the kill, and red deer 83%. This comes within 1% of the proportion of the two species shown by the roar data (though the latter represent males only).

The figures for average proportion of sika to red in the kill differ significantly

between the blocks ($P < .001$). The highest proportion of sika (49%) was recorded in Block 1, and the lowest (14%) was from the western Block 3. This suggests that the greatest preference of sika is for the eastern flank of the Kaweka, and confirms the roar pattern indicated in Fig. 14.

The increased proportion of sika to red deer between 1962-63 and 1964-65 suggested in the roar data is also indicated by the proportions killed in the control operations from 1959-71. For the three blocks over all (Table 4, Fig. 15), the proportion of sika increased significantly with time ($t = 2.41$; 8 df; $p < .05$). Both sources of data suggest that the composition of the deer population in the Kaweka is slowly shifting from an order of five red to one sika deer towards an increasing proportion of sika deer.

TABLE 4—Kill figures from control operations and proportion of sika and red deer 1959-71 in Tutaekuri (1) Mohaka (2) and Ngaruroro (3) Hunting Blocks

Year	Sika deer				Red deer				Total Sika and Red	Ratio Sika : red deer		
	1	2	3	Total	1	2	3	Total		1	2	3
1959-60	42	13	13	68	99	16	375	490	558	0.42	0.31	0.03
1962-63	15	14	36	65	62	39	195	296	361	0.24	0.36	0.18
1963-64	49	39	59	147	434	222	610	1266	1413	0.11	0.18	0.10
1964-65	82	18	45	145	99	110	349	558	703	0.83	0.16	0.13
1965-66	52	29	28	109	70	68	369	507	616	0.74	0.43	0.08
1966-67	32	45	66	143	61	184	609	854	997	0.52	0.24	0.11
1967-68	55	15	68	138	222	126	492	840	978	0.25	0.12	0.14
1968-69	74	28	100	202	124	71	482	677	879	0.60	0.39	0.21
1969-70	29	93	72	194	79	322	401	802	996	0.37	0.29	0.18
1970-71	35	81	85	201	44	350	344	738	939	0.80	0.23	0.25
	465	375	572	1412	1294	1508	4226	7028	8440	0.49	0.32	0.14

N.B. Only total kill figures are available for the Kaweka control operations during 1960-61 (81 sika and 454 red) and 1961-62 (95 sika and 763 red).

DISCUSSION

In this paper criteria were sought to differentiate between sika and red deer where they co-exist. Morphological characteristics which have been thought to be diagnostic of sika deer alone (such as formation of antlers, hair of the ear, and of the metatarsal gland, skull sutures, and even the distinctive white rump patch) were found to be not necessarily constant. The discriminant function analysis carried out on selected characters of the sika/red deer autopsy data, however, show that field identification of the two species can be more than adequate, even allowing identification of possible hybrids (Fig. 3). Initial diagnosis of adult deer from general appearance and pelage can now be substantiated by using Table 1, which shows for the selected characters the means of

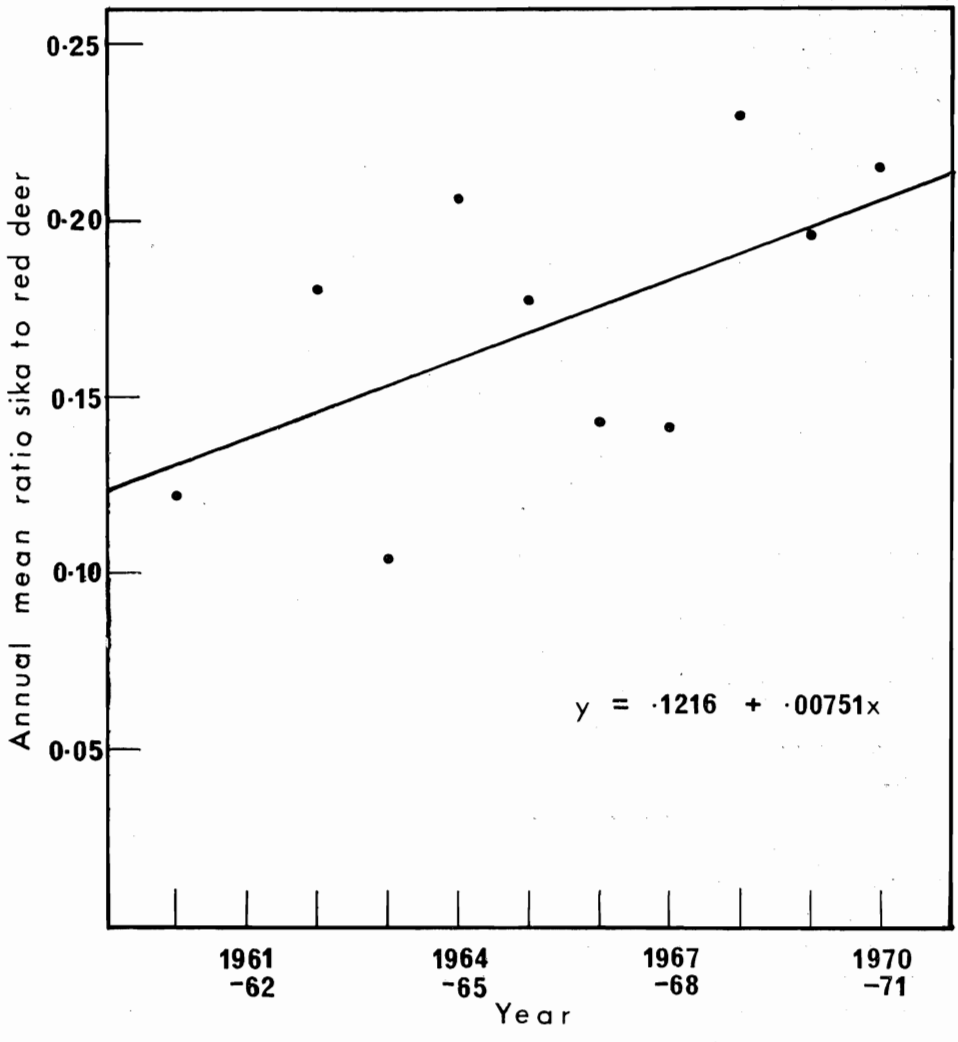

FIG. 15—Ratio of sika to red deer calculated from control operation data (1959-71).

animals falling within the sika membership group. With the exception of the tail (both hair and skeletal structure) all measurements are considerably less than those for red deer and they approximate to estimates given by experienced hunters, particularly the height at shoulder. All are field measurements taken over the skin, so that the head length exceeds quite appreciably that of the cleaned skull, the measurement required for a trophy head. Ear, rear foot, and hoof to metatarsal gland lengths are good diagnostic features more readily taken in the field than the larger measurements.

There is strong evidence for the existence of several subspecies. Observations in the Oamaru Valley showed different spotting patterns and an occasional white throat patch.

A 2:1 ratio of black to red antler velvet also suggests that there are at least two subspecies present.

To some degree, the probable occurrence of more than one type of sika, and possibly of red deer (though nominally Windsor strain (Donne, 1924; Logan and Harris, 1967), in the population sampled complicates any simple conclusion on hybridism between the two species. Sika/red deer hybrids have been recorded for captive and wild animals in Britain (Whitehead, 1950, 1964) and hunters in New Zealand have debated the question of hybridism for half a century (Douglas, 1952; Kiddie, 1962). Only two females and no males were considered to be hybrids by the hunters in the field diagnoses. It is surprising that so many animals, particularly putative sika, should be assigned a relatively low group membership probability status in the discriminant function analysis. As shown in Figs. 2 and 3 only one male and three female red deer are given red deer membership status of less than 99%. Conversely, 9 female and 8 male sika are ranked in this species at less than 99%. Furthermore, four females and two males in the sika grouping are placed at less than 90% probability. This distribution strongly implies that whereas putative red deer are clustered with better than 99.99% group membership, putative sika are strung out across the group membership spectrum suggesting both intra-specific variation and a hybrid gradient. While it can be concluded that hybridism occurs, more research is necessary before the proportion of hybrids can be determined. The dispersal distribution of putative sika (also seen in antler patterns and intensity of spotting) may be worth careful study from the point of view of both hybridism and intra-specific variation. There is, however, the possibility that bias in sampling resulting from behavioural traits of the two species, and differences in the ease of hunting them, may prohibit definitive answers to the question of degree of hybridism between the two species.

Sika deer were released in forest/shrubland where they met the conditions required for successful colonisation, outlined by Keeton (1967). Unlimited habitat containing an abundance of palatable food was available and the climate was less rigorous than that of their origin, so that adjustments for survival and reproduction would have been minimal. Little competition would have been met because of the absence of already established indigenous species. Interaction with red deer for food and territory would also have been negligible as the preference of sika for the shrubland-ecotone and tussock grasslands would minimise the use of forest resources already depleted by red deer. In addition, observations in the Oamaru Valley revealed no active aggression between the two species so that sika would have been able to disperse unhindered through red deer habitat. Ecological opportunity for the establishment and dispersal of sika was ample therefore, and access throughout the large area of similar territory (*see* Fig. 13) was unimpeded by any major physical barriers.

It would appear that the assumption made from McKelvey's (1959) report that sika could degrade the forest beyond a level of damage caused by red deer is a misinterpretation of the situation. Observations made in the course of the present study indicate that sika are predominantly grazers (Davidson, in press).

Dispersal can either be induced by population pressure, i.e., density-dependent (Keeton, 1967), or the result of the innate urge of animals to leave their place of origin on reaching puberty, i.e., density independent (Howard, 1960). As sika dispersed from

their liberation point more quickly than could have been induced by population pressure, it is likely that their spread was largely the result of innate migratory behaviour, or the product of diffusion in the manner described by Caughley (1970) for thar in New Zealand. There has been some suggestion that sika spread only after modification of the habitat by red deer (Wodzicki, 1961; Dasmann, 1964). Red deer dispersing from liberations in the eastern Ruahine (1883), Tongariro and Galatea (1897) and western Ruahine (1902), recorded by Logan and Harris (1967), are unlikely to have reached sufficient numbers to have depleted the northern Kaimanawa forest before the liberation of sika deer in 1905. No evidence has been found for the presence of red deer in the Kaimanawas before this date. As late as 1931, Jordan (1931a) records that only on one occasion did he encounter a red deer stag in sika territory, though red deer country was on all sides. In addition, McKelvey (1957) suggests from tree ring data that it is likely that the onset of moderate deer damage to forest in the vicinity of Merrylees clearing (the site of sika liberation in 1905) occurred as late as 1922, which appears to rule out the possibility of prior depletion by red deer. It is postulated that red deer were not occupying the northern Kaimanawas when sika were introduced and that they were subsequent intruders in sika-occupied territory. A further suggestion that wild dogs known to have roamed the Kaimanawa forest in the early years may have contributed to the spread of sika (Logan, 1957; K. East, pers. comm.) can be of little significance, if true.

Sika deer have now spread over an area of at least 11,000 km^2 (*see* Table 2). In this study hide observations on the Oamaru Valley flats from 1964-6 gave a ratio of sika : red = 6 : 1, which corresponds with the 6 : 1 ratio observed in the same area in 1960-1 (Daniel, 1966). Autopsy records in 1963-6 from an area of 100 km^2 surrounding the Oamaru River-Kaipo Stream confluence, and comprising elements of the northern Kaimanawa/northern Kaweka/western Ahimanawa areas, gave a sika : red ratio of 3 : 1. Outside these areas the proportions are reversed and red deer become dominant.

A deer skin record for the nearby region at the head of the Ngarororo River shows that of 417 deer shot between September 1955 and September 1959 only 12 were sika (E. G. Nutt, pers. comm.). Similarly, data from roar plottings and control operations in the eastern Kaweka show a small ratio of sika to red deer (Tables 3 and 4).

Although records of sika dispersal are fragmentary, there are more data available than when Caughley (1963) estimated an annual rate of 1.6 km by measuring the maximum distance between point of liberation and furthest breeding colony, divided by the number of years. For the decades up to 1950 the equivalent rates estimated for breeding colonies in this study varied between 0.6 km and 0.9 km (Table 2). After 1950, faster rates were calculated, 1.5 km for 1951-60, and 1.4 km for 1961-70. All these rates come close to that calculated by Caughley. The same criticism of an implied constant rate of expansion (Caughley, 1970), however, is also valid for the technique used in this study to estimate dispersal.

The apparent acceleration of dispersal shown for the 1951-70 decades (which occurred particularly to the north-west) is open to many interpretations, not least of which is that hunters and others were becoming more familiar with the sika species, resulting in increased sighting records. As dispersal proceeded, sika were moving further into areas of human activity, some of long standing. Early destruction of forest led to

the development of the shrubland corridors so well exploited by sika, in which their advance could have been accelerated. In western Taupo, extensive logging took place, a state highway was constructed, and the large area of shrubland between the Hauhangaroa forest and Lake Taupo was developed for farmland. At this stage, human activity, including increased skills in hunting sika, may have had an effect similar to population pressure, forcing the deer to move westwards where their dispersal would have been facilitated because of prior depletion of the forest by red deer, as was also envisaged by Logan (1957). Today, sika are found on the forest margins west of the Hauhangaroa and Rangitoto Ranges, and it is likely that they will continue to spread west and north into indigenous protection forest. However, because of the rapid development of the former wasteland habitat of sika into farmland and exotic forest it is difficult to predict from the earlier patterns other directions in which sika dispersal is likely to take place.

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APPENDIX I

Autopsy Methods

Body measurements were taken over the pelage with a flexible steel millimetre tape:

Tail length	— from base of tail (coccygeal-lumbar junction) to tip of last (distal) vertebra.
Head length	— from cranial (anterior) point of exposed premaxillae dorsally over curve of head to lambdoidal ridge (occipital crest). N.B. Not comparable to measurements taken over cleaned skulls as for trophies, **see** Douglas (1959).
Ear length	— from base of ear notch to distal tip.
Rear foot length	— from tip of hoof to tip of heel, as Wildlife Society (1957).
Hoof/Metatarsal length	— from tip of rear hoof to metatarsal gland.
Height at shoulder	— from front hoof tip to backbone between scapulae in a straight line.
Chest (heart) girth	— circumference of chest immediately posterior to the front legs, as Mitchell (1971).
Body length	— from anteriormost point of rhinarium to base of tail in a straight line.

APPENDIX II

References for Dispersal of Sika Deer

1.	1930	Holmes (1930)
2.	1930	Logan (1957)
3.	1937	New Zealand Department of Internal Affairs Annual Report
4.	1938	E. Wilson (pers. comm.)
* 5.	1939	Fraser (1939)
6.	1940	Kiddie (1962)
* 7.	1940	R. H. Hartree (pers comm.)
8.	1940	L. T. Pracy (pers. comm.)
* 9.	1946	Logan (1957)
* 10.	1947	P. C. Logan (pers. comm.)
11.	1947	Macgregor (1947)
12.	1949	Douglas (1949)
13.	1953	M. Robson (pers. comm.)
14.	1954	Rye (1954)