DECLINES IN POPULATIONS OF PEREGRINE FALCONS AND THEIR SEABIRD PREY AT LANGARA ISLAND, BRITISH COLUMBIA

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The Peregrine Falcon (*Falco peregrinus pealei*) population on Langara Island, British Columbia, has been known to naturalists and ornithologists for over half a century. This paper will outline some of the recent changes in the size and productivity of this population and of its prey population, and the possible causes of the changes. On the Queen Charlotte Islands (Q.C.I.; fig. 1), the Peregrine Falcons are resident year round. Their presence is closely linked to that of large numbers of potential prey in the form of seabirds which breed in spring and summer in burrows along the coast.

SIZE OF THE FALCON POPULATION

Green (1916) counted "thirteen eyries at the north-west corner of the main island [Graham Island] and on the rocky shores of Langara Island, just across Parry Passage." From one vantage point on Langara, Allan Brooks (1921) heard three broods calling and wrote (1926) "in the breeding season one is never out of hearing of the birds . . . and probably thirty-five pairs nest on the twenty-five miles of coast-line of this small island alone." In 1937, Brooks wrote to Joseph Hickey (J. Hickey, pers. comm.) that "On Langara (North) Island, which is only 8 miles long by 4 at its widest part, there are probably 40 nests occupied. In 1936, over 20 of these were climbed to by a visiting naturalist." Unfortunately, neither Brooks nor Green clearly indicated the portion of the coastline he covered, but both were greatly impressed with the size of the falcon population.

In the 1950s, during five different years, Frank Beebe (1960) visited Langara Island. He checked almost two-thirds of the coastline in most years. C. J. Guiguet provided information on three additional occupied sites in the area Beebe did not visit. In 1952 Beebe recorded 13 occupied sites (Beebe 1960: table 2); if the three sites Guiguet reported were also occupied, then 16 were known in the early 1950s (fig. 2). For comparative purposes it is best to consider only the part of the island that Beebe visited most frequently. In 1958, Beebe's study area contained five unoccupied sites, seven occupied sites, and one unchecked site that almost certainly was occupied. When Beebe's data (1960: table 2) are reorganized to allow comparison between the different years (cf. table 1), it is evident that between 1957 and 1958 the number of unoccupied sites in his study area increased suddenly from one or two to five or six of the 13 occupied in 1952.

In 1966, 1967, and 1968, the British Columbia Fish and Wildlife Branch surveyed the Q.C.I. for falcon eyries. Blood (1969) reported that "As only seven active eyries could be located at Langara in each of the years 1966 and 1967, and only five in 1968, it is apparent that there has been a significant decline in peregrine breeding densities there."

Between April 1968 and June 1973, R.W.N. and his wife spent 24 months on Langara. In these years the falcon population fluctuated between 5 and 6.5 territorial pairs. In 1969 two pairs contained yearling females and produced no eggs or young. One unpaired adult male remained on his territory for three breeding seasons, one adult male was unpaired through the 1972 season, and another was unpaired in 1973 (fig. 3, table 2). In the portion of the island covered by Beebe, only 25% of the former number of pairs was present during 1968–73 (fig. 4). On the remainder of the island there were (1973) another 3.5 pairs, compared with perhaps 8–10 pairs in the early 1950s, making a total breeding population of ca. 21–23 pairs in the early 1950s, approximately three and a half times the number present in recent years (fig. 4).

Before discussing the recent productivity of the falcons, we should note that we consider the present falcon population at Langara to be saturated or incapable of holding any (or many) more territorial pairs; evidence for this will be presented below.

PRODUCTIVITY OF THE LANGARA PEREGRINES

Clutch size. The mean size of 11 clutches observed early in incubation in recent years at Langara Island, was 3.8 (one nest with 5

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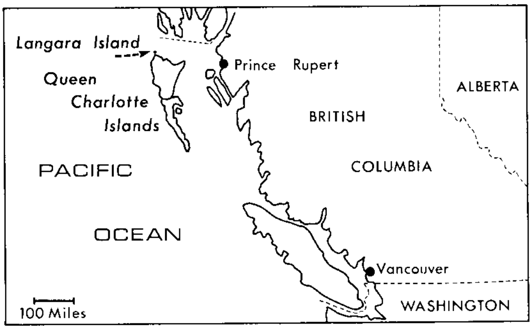

FIGURE 1. Langara Island and the Queen Charlotte Islands off the coast of British Columbia.

eggs, three with 3, seven with 4). This appears normal. Bond (1946) reported that eight clutches of *pealei* averaged 4.5 eggs, and Brooks wrote to Hickey (J. Hickey, pers. comm.) that "the number of eggs was 4 in nearly every case" in 1936 at Langara.

Egg loss. Ratcliffe (1970:68) noted that only 4 of 100 pre-pesticide clutches of Peregrines in Britain lost one or more eggs during incubation. In contrast, of 12 clutches followed through all or part of incubation at Langara from 1968–73, five (42%) lost eggs. One entire clutch (3 eggs) was lost when a new female took over a site (a rare event). Four clutches (33%) lost single eggs apparently by accidental breakage (4 of 12 clutches differ significantly from expected; binomial test, $P < 0.001$). The single eggs which disappeared account for 8.9% of all eggs laid. The combined losses (7 of 45 eggs) represent 15.6% of the eggs laid and may be important to the population (table 3).

Failure to hatch. Of the 38 eggs remaining in the 11 clutches, 9 (20.0% of the eggs laid) did not hatch. Five of these were salvaged. Two, from separate nests, held dead embryos, and three (of a clutch of five) showed no development. One additional nest, not followed through incubation, contained one egg with no development, one with a dead embryo, and one 8 to 10-day-old nestling.

Hickey (1942:188) noted that "several correspondents state that infertility of one egg in every set is 'not uncommon'... an analysis of ninety-five records by egg collectors shows that only 7% of their sets contained one infertile egg, while 4% of such sets were addled." He adds, "... in the British Isles, H. A. Gilbert (in litt.) writes: 'It is very

TABLE 1. Occupancy and productivity of Peregrine Falcon sites, Langara Island, 1952–1958.[a]

Site	1952	1955	1956	1957	1958
Radar Site	2ff	2ff	NC	3F	3 lg
McPherson Pt.	4 lg	3 lg	3F	3F	Occ(0)
Explorer Bay	Occ–nc	Un	NC	NC	Un
Andrews Pt.	2sm	3 lg	3F	2F	Un
Coho Pt.	3E	3 lg	Un	Un	Un
Dadens	2F	Occ(0)	2F	2F	2F
Burial Cave	Occ(1♀)	Occ(1♀)	NC	2F	Un
Iphigenia Pt.	Occ–nc	4ff	Occ–nc	3F	3F
First Pinnacle	Occ–nc	3F	2ff	2F	2 lg
Twin Pinnacles	Occ–nc	2E	3 lg	3F	2E
Third Pinnacle	Occ–nc	1ff	1ff	2ff	1ff
Fourth Pinnacle	Occ–nc	Un	NC	2F	Un
Cox Island	4E	4ff	2 lg	?F	NC
Summary					
Not Checked	0	0	4	1	1
Checked	13	13	9	12	12
Total occupied	13	11	8	11	7
Occ. by pairs	12	10	8	11	7
No. of young: F	1 (2y)	1 (3y)	3 (8y)	10 (22+y)	2 (5y)
ff	1 (2y)	4 (11y)	2 (3y)	1 (2y)	1 (1y)
lg	1 (4y)	3 (9y)	2 (5y)	0	2 (5y)
sm	1 (2y)	0	0	0	0
E	2 (7E)	1 (2E)	0	0	1 (2E)
Occ(0)	1	2	0	0	1
Occ-nc	6	0	1	0	0
Unoccupied	0	2	1	1	5
Un/checked	0/13	2/13	1/9	1/12	5/12
Probable Un/checked	0/13	2/13	3/13–2/13	2/13	5/13

[a] Data derived from Beebe (1960:table 2 and fig. 8). E = eggs. y = young. sm = small downies. lg = large downies. ff = fully fledged. F = flying young. Occ(0) = occupied, no production. Occ–nc = occupied, eyrie not checked. Occ(1♀) = single adult female at site. NC = site not checked. Un = unoccupied. Visits made on 2, 8, 19, 20, 17 June, respectively.

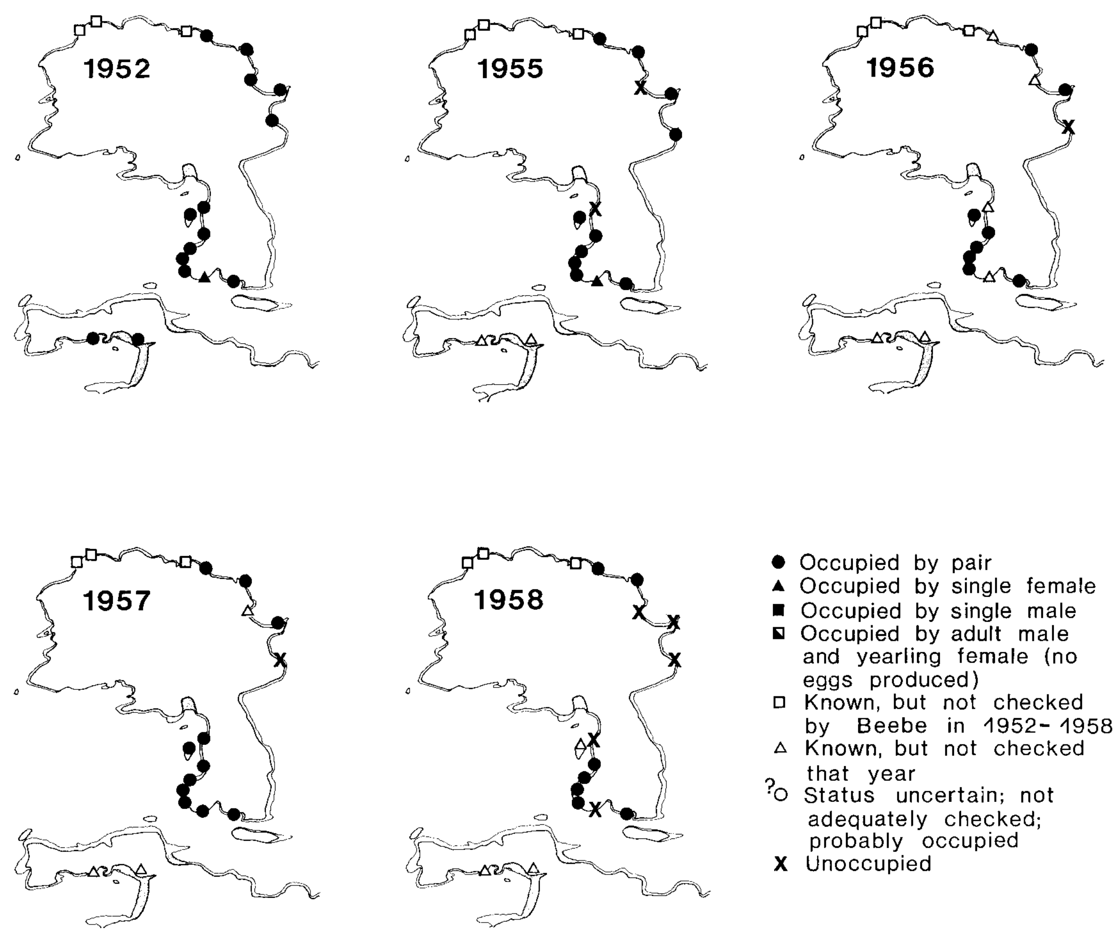

FIGURE 2. Sites occupied by Peregrine Falcons on Langara Island, 1952–58. (Derived from Beebe 1960.)

rare to find an infertile egg—and I am convinced that at least 95% . . . are hatched unless cracked by falling stones or upset by human interference'."

A hatching failure of 20% of the Langara eggs appears to be a clear increase over previous years. Of the 11 clutches followed, 6 (54.5%) contained one or more eggs which failed to hatch. This differs significantly from Hickey's (1942) value (test of equality

TABLE 2. Productivity of Peregrine Falcons on the whole of Langara Island, 1968–73.[a]

Year	1968	1969	1970	1971	1972	1973	Totals & Means
Total Occupied sites	5[b]	6	6	7	7	7	38
Occ. by single ♂	0	0	1	1	2	1	5
Occ. by pairs	5[b]	6[c]	5	6	5	6	33
Sites with No F	1[d]	3	1	3	3	2	13
Pairs with No F	1[d]	3[c]	0	2[e]	1[f]	1[g]	8
Pairs with F	4[h]	3	5	4	4	5[i]	25[h,i]
No. of F produced	9[h]	5	11	11	10	11[i]	57[h,i]
Mean F/Occ. site	1.80	0.83	1.83	1.57	1.43	1.57	1.50
Mean F/pair	1.80	0.83	2.20	1.83	2.00	1.83	1.73
Mean F/successful pair	2.25	1.67	2.20	2.75	2.50	2.20	2.28

[a] E = eggs; y = young in nest; F = flying young.
[b] Probably one more with unknown F; not adequately checked; see fig. 3.
[c] Two pairs of adult males and yearling females, no production; another pair had 3E fail to hatch and 2y die.
[d] Behavior suggested early loss or no production (not included in "Pair-success" in text).
[e] One pair lost its 1y; one pair lost its 3y.
[f] Lost 3E when new ♀ ousted old ♀.
[g] New ♀; apparently produced no eggs.
[h] Includes one site which had its three large nestlings removed illegally.
[i] Includes a pair with 2y about half grown when observed in late June 1973 (not included in "Fledglings per occupied site" in text).

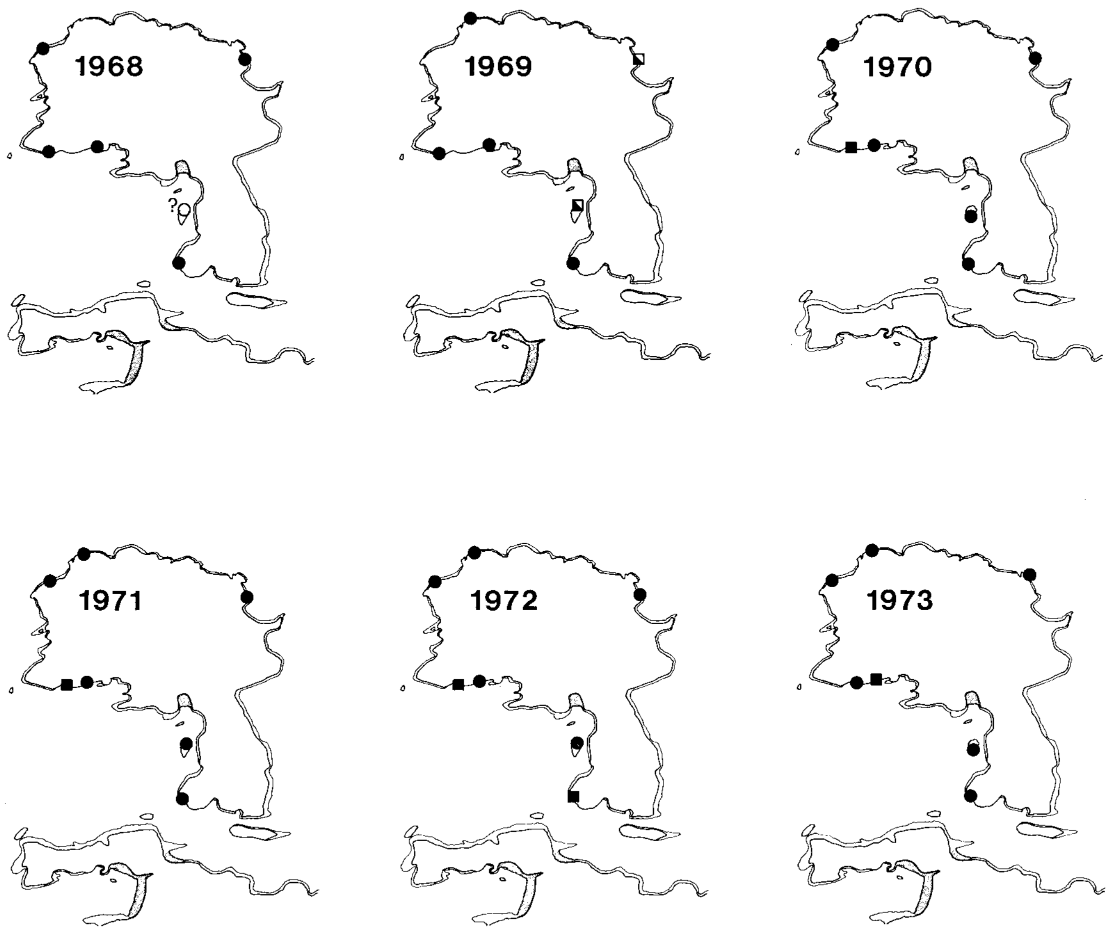

FIGURE 3. Sites occupied by Peregrine Falcons on Langara Island, 1968–73. (Symbols as in fig. 2.)

of two percentages, $P = 0.002$; Sokal and Rohlf 1969). The 35.6% combined loss of addled eggs and eggs that disappeared is substantial.

Nestling losses. Ten nestlings were known to have died on the ledges or vanished, and presumably died. This represents a loss of at least 14.9% of the nestlings and 9.6% of the eggs laid (table 3). Two fledglings died in their first week of flying.

Brood size. During the 1950s, counts in

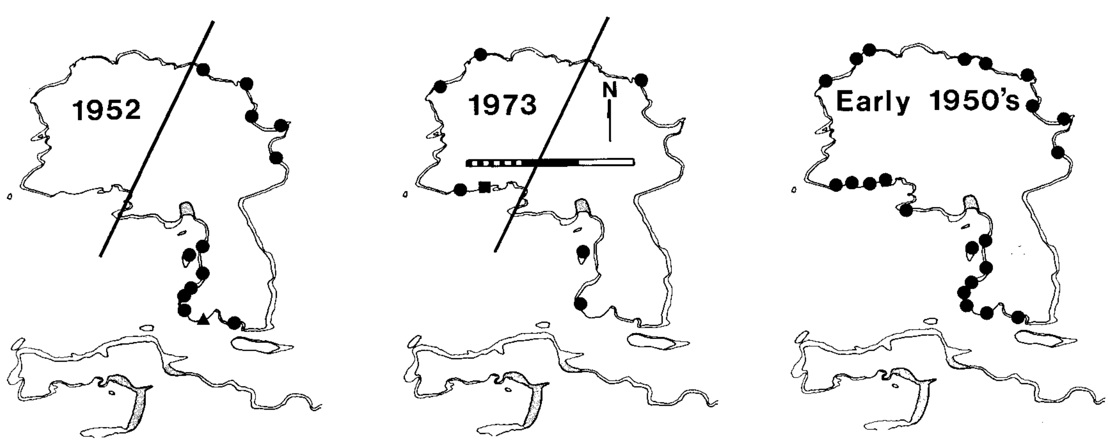

FIGURE 4. Sites occupied by Peregrine Falcons on Langara Island, 1952 (left), and 1973 (center). (Symbols as in fig. 2; scale is in miles and tenths.) The area studied by Beebe (to the right of the diagonal) in 1952 had four times the number of occupied sites found there in 1973. The probable occupancy by Peregrines of the whole of Langara Island in the early 1950s is also illustrated (right).

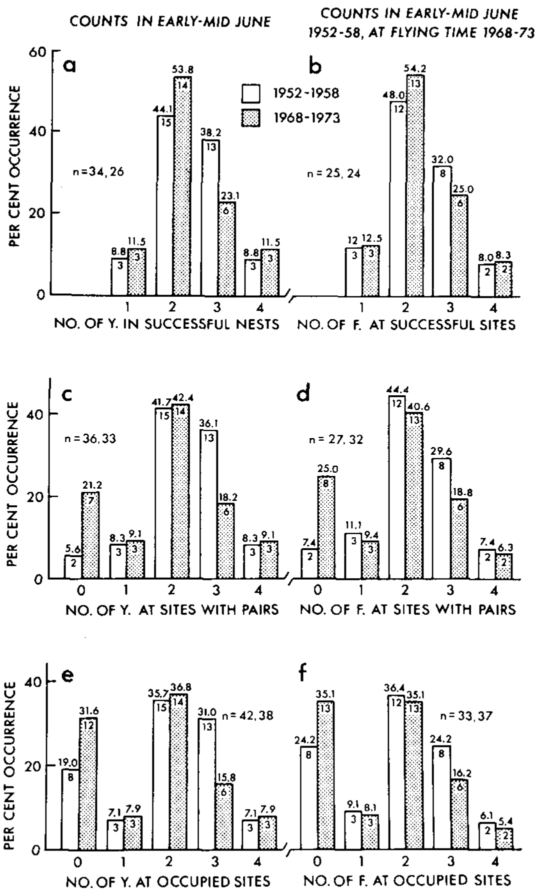

FIGURE 5. Productivity of the Langara Island Peregrines. Comparison of 1952–58 and 1968–73 on the basis of percent of nests or sites with given numbers of young. Y = young observed in nests or flying. F = "fully fledged" or flying young. Numbers atop bars are percents of sites with the given brood size. Numbers within bars are the actual number of sites observed with the given brood size. n = sample sizes in 1952–58 and 1968–73, respectively.

a vs. b considers only successful nests and suggests a decline in broods of 3 and an increase in broods of 2 in 1968–73. c vs. d includes only territorial pairs (excluding four clutches unhatched when observed in June in the 1950s) and shows a decline in broods of 3 and an increase in pairs that failed (broods of zero) in recent years. e vs. f includes sites occupied by single falcons and assumes that eggs observed in June in the 1950s represented pairs producing zero young (i.e., failures in the 1950s may be over-represented); again the recent decline in broods of three and increase in sites failing are evident.

early and mid-June revealed a mean of 2.47 young falcons per successful nest at Langara (34 nests and 84 nestlings or flying young; calculated from Beebe 1960: table 2). In 1968–73, similar counts in early to mid-June revealed 2.35 young falcons per successful nest at that stage of the breeding cycle (26 nests with 61 young). These differences are not statistically significant (t-test, $P > 0.50$), although recent successful nests contain almost 33% fewer broods of three and almost 25% more broods of two (fig. 5a) than in the 1950s, apparently reflecting recent egg and nestling losses and hatching failures.

Fledglings per successful nest. In the 1950s, Beebe observed 59 "fully fledged" nestlings and flying young falcons at 25 nests (table 1), for a mean of 2.36 fledged falcons per successful nest. During 1968–73, the comparable figure was 2.29 (55 fledglings at 24 nests). This difference is not statistically significant ($P > 0.50$), but it does reflect the recent losses noted above (fig. 5). Comparable figures (young reared per successful pair) were 2.4 in Cornwall (24 nests, 1930–40; Ryves 1948, cited in Hickey and Anderson 1969), and 2.5 (16 nests, 1939–40) in a 26,000 km^2 area of Connecticut, New York, New Jersey, and Pennsylvania (= "around New York"; Hickey 1942).

Pair success. If we include eggs still unhatched in June as inviable, Beebe's data suggest that as many as 14.6% of the pairs may have failed to rear young in the 1950s ($N = 41$ nests, 35 with young, 4 with eggs, 2 empty). If the four nests with eggs actually were successful, then only 4.9% of the pairs failed.

In 29 breeding attempts known to have produced eggs in 1968–73, four (13.8%) failed to produce flying young. If we add two pairs in which the females were yearlings and one in which the female was a new adult, all of which produced no eggs, the proportion of pairs failing reaches 21.9%. If 14.6% of the pairs failed during the 1950s, the difference from recent years is not statistically significant (test of equality of two percentages, $P = 0.4$). If, however, only 4.9% of the pairs failed in the 1950s the difference is significant ($P = 0.03$).

Fledglings per occupied site. In recent years (1968–73) the production of fledglings per occupied site (with known outcome) at Langara has ranged from 0.83 to 1.83 ($\bar{x} = 1.49$; table 2). It is difficult to derive a comparable figure from Beebe's data. An estimate of 1.79 fledglings per occupied site is obtained by considering the 25 nests with (59) fully fledged or flying young (table 1), and the two occupied sites with no young, the two occupied sites with single females, and the four nests with eggs not expected to hatch. The difference between 1952–58 and 1968–73 is not significant ($P > 0.25$), but figures 5c–f do show the increased proportion of failures

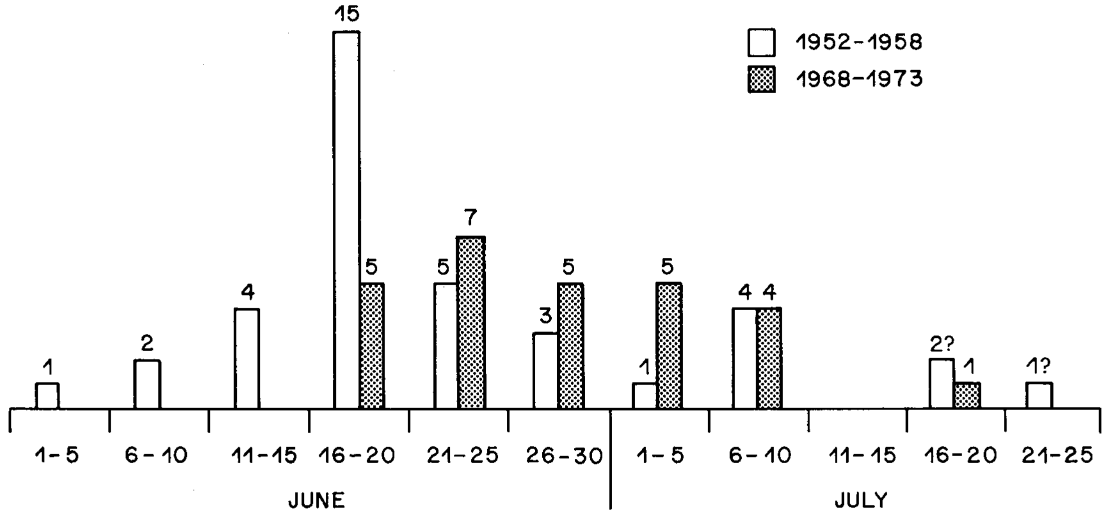

FIGURE 6. Comparison of dates of first flights by broods of Peregrines at Langara Island in 1952–58 and 1968–73. (For explanation, see text.)

and the decreased proportion of broods with three young in recent years. It is of interest to compare the Langara production with that in Cornwall (Ryves 1948) where 1.7 young were reared per occupied site, and "around New York" (Hickey 1942) where the number was 1.2 (1.5 in 1939; 0.7 in 1940, a "bad spring").

In conclusion, the Langara Peregrine Falcons are reproducing presently at a rate that seems slightly depressed from 20 years ago. The number of eggs per clutch appears to be normal, but an unusual number of eggs disappear (apparently a majority due to accidental breakage) or fail to hatch. Some nestlings die, and fewer nestlings and fledglings are found per nest. Of all the eggs laid, only 54.8% produce flying young.

FLYING DATES OF YOUNG FALCONS

Hatching and egg-laying dates can be closely approximated from the date of the first flight of young falcons. The dates of the first flights observed in 1968–73 are shown in figure 6. In recent years the first flights of broods have taken place usually at 41–43 days of age. Knowing this, we calculated the dates of first flights of Beebe's broods assuming that (1) eggs he saw would have hatched in the next few days (they actually may have been

TABLE 3. Known losses of eggs and young of Peregrine Falcons at Langara Island, 1968–73.

Reproductive phase & type of loss	Eggs or yng at or near start of phase	Eggs or yng at end of phase	Eggs or yng lost in phase	Clutches or broods involved	Loss as % of eggs laid	% of eggs surviving at end of phase
Egg-laying	0	15	0	4	0.0%	100%
Incubation	45			12		
Clutch losses			3	1	6.7%	
1 egg losses			4	4	8.9%	
Unhatched			9	6	20.0%	
Total			16	8	35.6%	
Survived		29		11		64.4%
Nestling	67[a]			28		
Brood losses			6	3	5.8%	
Single losses			4	4	3.8%	
Total			10[b]	7	9.6^{+}%[b]	
Survived		57[c]		25		54.8^{-}%
Early Fledgling (1wk.)	57[c]			25		
Brood loss			2	1	1.9%	
Survived		55		24		52.9^{-}%

[a] Minimum number known to have started this phase; unknown nestling losses may have occurred prior to observations at some sites in some years due to varying coverage.
[b] Minimum number; known to have died during this phase.
[c] Includes two half-grown nestlings at one nest at last check.
NOTE: Of the data presented, possible loss caused by our disturbance is a brood of two small nestlings; however, circumstances surrounding their deaths suggested that factors other than our disturbance were involved. Most of the above data were gathered by observing nests from distant vantage points and blinds.

inviable or laid as replacement clutches; we omitted the latest clutch); (2) "small downies" were 5–10 days old; (3) "large downies" were about 21 days old; (4) "fully fledged" nestlings were 36–40 days old; and (5) the date on which a "flying" young falcon was observed was the day of its first flight. We almost certainly have plotted (fig. 6) Beebe's data too far to the right because "flying" young may already have been flying for two weeks or more when Beebe observed them.

For recent years the mean date of first flying is 28 June. In the 1950s it was 21 June or earlier; these dates differ significantly (t-test, $P < 0.01$). However, if we consider Beebe's three early-June clutches to be first clutches which later hatched, and include them, then the mean flying date in the 1950s is 23 June or earlier and does not differ significantly from the 1968–73 date ($t = 1.52$; P at $0.10 = 1.67$).

The close proximity of breeding pairs in the 1950s may have stimulated earlier egg-laying in the manner suggested by Darling (1938). The data from the colony of captive kestrels at the Patuxent Wildlife Research Center tend to support this (Porter and Wiemeyer 1972). Alternatively, in recent years biocide content may have influenced the egg-laying dates of the falcons. Jefferies (1967), Peakall (1970), and others have pointed out that DDT in the diet can delay ovulation. Risebrough et al. (1970) suggested that polychlorinated biphenyls (PCB) also may cause such effects. Porter and Wiemeyer (unpubl. data, cited in Porter and White 1973) found that DDT delayed ovulation in American Kestrels (*Falco sparverius*), and Porter and White (1973) suggested that the same phenomenon may have occurred in wild Peregrine Falcons. The Langara data appear to confirm this.

ADEQUACY OF PRESENT PRODUCTIVITY

Despite the facts that (1) the present falcon population is much reduced from 15–20 years ago, (2) two sites in 1969 were occupied by yearling females, (3) two territorial males in 1972 were unable to pair, and (4) the turnover of adult females is greater than that of adult males, production and recruitment in the Langara population appear sufficient to maintain, perhaps even increase, the present breeding population. Facts supporting the impression that the present population is saturated and that productivity is adequate to maintain this reduced population are that (1) productivity falls within the bounds of that found elsewhere before the introduction of DDT; (2) in 1970–71 a new pair of adults became established in an alternate site of another pair; (3) in the spring of 1971 and 1972 yearling falcons "tested" adults at most occupied sites; (4) in 1972 a new adult female evicted an incubating female from the territory the latter had held for three seasons; (5) in 1973 adult females in three of six pairs were new.

CAUSES OF THE FALCON DECLINE

OVERHARVEST?

During the 1950s, many nestling Peregrines were harvested from Langara, the total in two years possibly exceeding 50% of production (McCaughran 1964). Since 1962, only a small number of nestlings has been removed, the last being three taken illegally in 1968 (they were presumed to have fledged in the calculations above). If overharvest caused the falcon decline, then 6 years of reduced or no harvest plus 5 years of total protection (1969–1973) should have permitted additional falcons to occupy territories vacated 10–15 years earlier. Such a recovery has not occurred.

BIOCIDES?

Nelson and Myres (unpubl. data) discuss the presence and origins of the substantial levels of biocides in the Langara falcons and their food chain. Addled eggs average 17.6 ppm DDE and 11.0 ppm PCB (wet weights; geometric means of 17.0 ppm and 7.6 ppm, respectively). Their eggshells have a mean thickness index 12.6% less than eggs taken pre-1947 on the Canadian west coast (reported by Anderson and Hickey 1972). These DDE levels and the degree of shell-thinning are more than half those at which other falcon populations have failed to maintain their numbers. Mercury levels (0.75 ppm and 0.73 ppm, arithmetic and geometric means respectively) also may be more than half that at which large-scale embryonic mortality occurs. On the basis of known egg-losses and known shell-thinning in recent years, we suggest that the depressed reproductive success up to hatching is largely due to the effects of pollutants.

The simultaneous death of all brood-mates has been recorded three times, at different eyries in different years. Parental neglect, infanticide, severe weather, critical shortage of food, and disturbance by man are not implicated in at least two of these cases. We believe that some pollutant acting through the mother predisposed the brood-mates to die either at some specific age or when subject in common to some stressful, not normally fatal, condition (e.g., rapid feather growth).

DECLINE IN THE ANCIENT MURRELET POPULATION

Numerous references in the literature describe the formerly huge numbers of Ancient Murrelets (*Synthliboramphus antiquus*) breeding on Langara Island. Unfortunately, very few estimate numbers in colonies or in staging areas offshore. For example, Green (1916:474) stated, "the whole island is a warren of Ancient Murrelets, and there are colonies of other sea-fowl at particular points and on adjacent islets, but the Ancient Murrelets predominate, and are killed by hundreds by the Falcons and by thousands by Indians." Darcus (1927:198), referring to Cox Island (SW of Langara), wrote "this island is literally honeycombed with the nesting burrows of Ancient Murrelets, Cassin Auklets [*Ptychoramphus aleuticus*], and Fork-tailed [*Oceanodroma furcata*] and Leach Petrels [*O. leucorhoa*]." Regarding Langara Island, Darcus (1930) also wrote, "CASSIN'S AUKLET. —Abundant, breeding all along the coast of Langara Island . . . ANCIENT MURRELET. —Abundant; the most abundant of the family on Langara Island, its nesting burrows being found as far as one-quarter mile from the sea." In the 1940s and 1950s these two species were still present in very large numbers (Beebe 1953, Drent and Guiguet 1961). Beebe (1960:169) remarked that "The numbers can only be described as astronomical."

In 1968–73 R.W.N. examined several of the Ancient Murrelet colonies on Langara both by day and night. Some evening counts also were made of Ancient Murrelets gathered in staging areas offshore from colonies. In 1970–71 S.G. Sealy studied Ancient and Marbled Murrelets (*Brachyramphus marmoratus*) at Langara and provided much additional information. The largest number of murrelets R.W.N. observed was 7857. They were counted by telescope from shore on 12 June 1972 (19:40 to 20:20). The murrelets were scattered over a large staging area at least 1.2 km offshore, south of the two southwest falcon sites. Murrelet incubation shifts usually are 3 days long (Sealy 1972). If the murrelets on the staging area that evening represented only those changing incubation duties that night, i.e., one-sixth of the population, then the total number using the colony may have been ca. 50,000 scattered along about 1.6 km of coast. C. J. Guiguet (unpubl. data) observed murrelets on the morning of 29 May 1952 in Parry Passage, just south of Langara. His "extremely conservative estimate" was 60,000 birds in an area only ca. 300 m × 300 m. Such numbers have not been seen anywhere at Langara in recent years, and we do not believe that the present population of the island can be as high as the 350,000+ murrelets that this 1952 observation suggested for one part of the island.

In several periods in May and early June 1968 and early June 1972 at a murrelet colony 0.8 km E of Langara Lightstation, the maximum number of adults heard fluttering into and out of the colony in one night was 125 and only seven murrelet chicks were seen and/or heard leaving the colony (3–4 June 1972). On 14–15 June 1971 R.W.N. counted in the colony just west of Henslung Bay on the north side of Parry Passage. In an area ca. 50 m in diameter, in the colony activity period (22:50 to 01:40 and 02:15 to 03:15) only 186 murrelets were counted fluttering into the colony, only 51 were heard taking off, and only 4 family groups and 12 unattended chicks were detected heading for the ocean. At the same location on 11–12 June 1972 (22:30–03:05), only 77 murrelets were heard fluttering into the colony, only 28 were heard taking off, and only ca. 15 family groups or chicks were detected leaving. These few counts and the impressions received in the colonies by night in recent years are far different from the observations reported from this island in the 1950s and earlier.

Since the 1950s, whole colonies or segments of colonies have been abandoned. The colony near Dadens, observed in 1966 by Campbell (1968, 1969), was essentially abandoned by 1970 (Sealy, pers. comm.). Cox Island was visited many times in 1969–73. R.W.N. spent the night of 4–5 June 1971 (calm, partially moon-lit) there searching for nocturnal seabirds. He heard a total of two Ancient Murrelets on the island and less than 20 murrelets calling in flight in the distance; he saw no nocturnal seabirds. This island is no longer "literally honeycombed" or "perforated by burrows" as reported by Darcus (1927) and by Drent and Guiguet (1961); indeed, few fresh or old burrows can be found.

Many thousands of murrelets still occur in the vicinity of Langara, but numbers in no way resemble those described from the 1950s and earlier. We estimate that murrelet numbers in 1968–73 may have been 10–20% of what they were in the 1940s and 1950s.

The Cassin's Auklet which was found "nesting over much of Langara's shoreline as well as on Cox and Lucy Islands adjoining" (Drent and Guiguet 1961) also has all but vanished from this area. Searches on Cox and Langara for nests of this species have been unsuccessful in recent years, and very few birds were seen on the ocean around these islands (Sealy, pers. comm.). Similarly, the two species of storm petrels reported nesting on Cox Island in the 1950s and earlier (Beebe 1960, Drent and Guiguet 1961) no longer appear in sizable numbers.

Causes of the Murrelet decline. Except on a local scale, we do not consider that predation by rats (present on the island for many years) or habitat changes have been of major importance in reducing murrelet and auklet numbers. In 1970–71 the productivity of the murrelets was good through departure of the young from the island (Sealy, pers. comm.).

Several fishermen at Langara have noticed many fewer surface aggregations of "shrimp-like plankton" in recent years as compared to a number of years ago. As the Ancient Murrelet and Cassin's Auklet feed largely upon euphausiids (Payne 1965, cited in Bédard 1969, Sealy 1972, White et al. 1973), these observations suggest that a reduction of the food supply has caused the murrelet and auklet declines although we know of no supporting quantitative data on plankton. Possible factors contributing to the decline are twofold. First, biocides may have affected the food chain. The zooplankton just mentioned depend ultimately upon phytoplankton. Decreased photosynthesis and growth have been found in some species of phytoplankton exposed to minute levels of DDT (Wurster 1968, PCB (Fisher et al. 1973), or mercury (Harriss et al. 1970, cited in Peakall and Lovett 1972). Because the murrelets do contain biocides (Nelson and Myres, unpubl. data), their zooplankton food, the phytoplankton, and the ocean water itself all must contain small amounts as well. We do not know whether biocides now present in the northeastern Pacific Ocean are sufficient to have damaged parts of the food chain below the level of the falcons, but it is possible.

The presence of biocides in the region of the Q.C.I. may be due to ocean currents (Nelson and Myres, unpubl. data). The Davidson Current, which flows northwest along the coast, is especially evident on the surface in winter (fig. 7) but is present off British Columbia year round (Sverdrup et al. 1942, Barber 1957, Fairbridge 1966, Bane 1969, Wyatt et al. 1972). The coastline of California lies within 2250 km of Langara Island. The use of the Pacific Ocean (and the Davidson Current) as a catch-all for chlorinated hydrocarbon wastes from southern California is known (Burnett 1971,

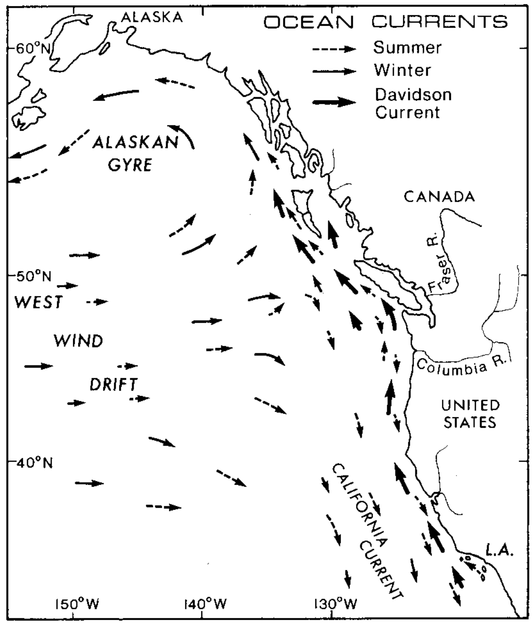

FIGURE 7. The Davidson Current in the northeastern Pacific Ocean, showing the probable route of biocides to the Queen Charlotte Islands. The lengths of the arrows approximate the relative speeds of the surface currents. L.A. = Los Angeles. (For sources, see text.)

Environmental Defense Fund 1971, Schmidt et al. 1971). In addition, a chlor-alkali plant and several pulp mills on the southwest coast of British Columbia have in recent years used mercury slimicides (Fimreite et al. 1971) and have put mercury into the ocean which may have reached the Q.C.I. Secondly, the plankton decline may have resulted from changes in ocean currents. The West Wind Drift (North Pacific Current, "Japanese Current") greatly influences the ocean off western North America. In the winter of 1956–57 warm surface water intruded along the British Columbia coast, lasting until the fall of 1958 (Tully et al. 1960). In the summer of 1957 and spring of 1958 the surface waters surrounding the Q.C.I. were 1–2°C warmer than the 30-year mean temperatures for those seasons. In the summer of 1961 a new anomaly approached North America (Tabata 1965); it remained until 1971 (Wick 1973) when the ocean (and weather) conditions returned to "normal." Bary (1963) and others have related the presence of certain species of plankton to certain ocean temperatures and salinities. This is important, as the Ancient Murrelets of the Q.C.I. are at the southernmost extent of their breeding range, perhaps limited by the abundance and availability of a "cold-water" plankton. The anomalous conditions of

1957–58 and the 1960s may have shifted the preferred plankton species northward or otherwise reduced its availability. Thus the decline of the Langara murrelets would be explained by a shortage of food brought about by changes in ocean currents.

If biocides are reducing food supplies of murrelets, then presumably Cassin's Auklets should be declining at colonies much farther south in their range where biocide levels presumably are higher; we are unaware of any collapses in more southern colonies. If the warming of waters off the Q.C.I. shifted much of the preferred food of the murrelets farther north, then the Cassin's Auklet might be increasing at Langara, which is near the northern extent of its range; warmer conditions might benefit it and its food species. However, this auklet has declined at Langara. These apparent contradictions are not yet explained.

FALCON TERRITORIALITY

In 1968–73, one site was occupied by a single male for three consecutive seasons, and two other sites each were held by single males for one season (fig. 3). At first, these observations suggested an insufficiency of females in the population. However, observations at these sites in 1972 and 1973 showed that the males were kept single by the females of adjacent pairs. In each case, the single male courted any apparently unattached female, but the neighboring female evicted all of his potential mates. In effect, the neighboring female occupied a double territory including that of her own male and that of the single male. The relationship may be described best as "pseudo-polyandry."

In 1971 a new pair of falcons attempting breeding took over one of two alternate sites of a resident pair. At about the time the new pair became established, the resident female disappeared. Perhaps with a new mate (or temporarily with no mate) the old male was unable to hold both sites. These two sites may again revert to one pair via pseudo-polyandry. The disappearance of a double-territory female in 1972 evidently allowed her neighboring male to acquire a female in 1973, even though the female that had kept him single in 1972 was replaced. In 1973 the status of two sites changed. The westernmost of these sites, occupied by a single male in the previous three seasons, was occupied by a pair. The eastern site, for the previous three seasons the home of a double-territory female, was held by a single male, kept single by the new female to the west. These observations indicate a somewhat flexible situation tending toward large territories by way of pseudo-polyandry. It is likely that when a single male dies, two territories suddenly become one large territory. We suggest that the small size, widespread distribution, and unusual territorial interactions of the present Langara Peregrine Falcon population are direct results of the considerable decline in numbers of the major (Ancient Murrelet) and minor prey species of the 1950s (see Beebe 1960). In relation to its food supply, the falcon population at Langara in 1968–73 appeared to be saturated.

In a calendar year a family of falcons will kill ca. 1000 murrelets. Therefore, in 1968–73 the number of Ancient Murrelets on the ocean around Langara Island was adequate to support, for a few years, the estimated 20+ pairs of breeding falcons on the island in the early 1950s. Nevertheless, in 1968–73 the 5 to 6.5 pairs maintained large territories and showed tendencies to expand these even further at the expense of neighbors.

The Langara falcons are resident, and only a single major prey species is available to them. This makes for a uniquely vulnerable predator-prey relationship, different from those described in a number of studies of avian feeding territories (e.g., Pitelka et al. 1955, Craighead and Craighead 1956, Schoener 1968). If murrelet numbers decline, the falcons cannot effectively switch to other prey nor can they move away from the area of scarcity. If these falcons were migratory, presumably territories would be established each spring in some proportion to the available food supply (see Schoener 1968). Were these falcons to maintain a large population during a murrelet decline and overharvest the murrelets, they would endanger their own survival in this area. Apparently, selection has produced year-round resident falcons with the ability to respond to the abundance of prey and to adjust their behavior (and thus their territory sizes) accordingly, permitting a conservative sustained-yield harvest of murrelets over the long term. The mechanism of pseudo-polyandry, combined with territorial expansion by males when neighboring single males die, seems to allow these resident falcons to reduce their breeding population in an orderly manner when the food supply dwindles due to other causes.

It seems certain that the proximate cause of the decline of the Langara Peregrine Falcons is the decline of their principal prey. The ultimate cause—biocides, alterations in ocean currents, or other factors—is yet to be determined.

OTHER Q.C.I. ALCID AND FALCON POPULATIONS

The falcon, murrelet, and auklet declines at Langara may appear unique because of the lack of historical data from elsewhere on the Q.C.I. Very little detailed work was carried out on either falcons or seabirds of other localities until the early 1960s. It is possible that the other parts of the Q.C.I. once had much larger populations of these seabirds and falcons than are present now. Studies on seabird distribution and colony size, such as those conducted by Summers (1974), and repeated inventories of falcon numbers, such as those of the British Columbia Fish and Wildlife Branch, will be needed for the Q.C.I. for some years to come.

PROSPECTS FOR IMPROVEMENT

Any sizable increase in the falcon population will require a considerable increase in the Ancient Murrelet population. If biocides have caused the murrelet decline by damaging their food supply, then recent moves to curtail the use and disposal of a number of biocides may lead to recovery of plankton stocks, then murrelets, then falcons. But over what timespan such a recovery may occur, we cannot judge. Harrison et al. (1970) suggested that the DDE contamination of the environment may worsen before it gets better, even with complete cessation of input of DDT into the environment, because of accumulation along food chains and the long life of these and related chemicals. We can only hope that the marine food chain cleanses itself before the coastal falcons are eliminated (either through shell-thinning or lack of food), and that other pollutants will not be introduced into the northeastern Pacific in the future.

If changes in ocean currents caused the murrelet and falcon declines, then the falcon population should have reached its low ebb in 1971 or 1972 because conditions returned to "normal" in 1971 (Wick 1973). There is some hope, then, that the Langara Island area may become repopulated (or more densely populated) by plankton, murrelets, auklets, and falcons. Again, there appears to be no precedent from which to gauge the length of time necessary for a repopulation trend to become recognizable, or for the Peregrine Falcons to achieve densities of 20 years ago.

If these two factors do not account for the murrelet decline at Langara, then the murrelets may continue to decline, reaching the point at which the falcons and possibly the murrelets themselves, will no longer breed in this region.

SUMMARY

The resident population of Peregrine Falcons at Langara Island, British Columbia, has been known for over half a century. The literature indicates that falcons were numerous here in the past. In the early 1950s the population was ca. 20 territorial pairs, but decline set in during the late 1950s. Between 1968 and 1973 the population fluctuated between 5 and 6.5 territorial pairs. Biocide levels in addled eggs were substantial. Eggshells were at least 11–12% thinner than pre-1947. Productivity was low; of the eggs laid, 15.6% vanished during incubation, 20.0% failed to hatch, and at least 9.6% gave rise to young that died as nestlings. Simultaneous death of all brood-mates has occurred several times; an internal mechanism, via a pollutant, is suspected. Compared to the 1950s, the falcons now experience more nest failures and produce somewhat fewer nestlings and fledglings per successful pair and per occupied site. The productivity appears to be adequate to maintain (perhaps even increase) the population, however; a number of yearlings are seen each spring, and some new adults have appeared. Territories are large, but birds tend to increase the size of their holdings at the expense of their neighbors. A form of pseudo-polyandry which has appeared at three sites prevents males from forming new pair-bonds after losing their mates.

The Ancient Murrelet, the principal prey species of the falcons, has declined greatly at Langara Island in the last 20 years. This decline appears to be linked to the murrelet's food supply. Either biocides have affected plankton (probably via the Davidson Current flowing north from California), or an anomalous intrusion of warm water near the British Columbia coast for most of 1957–71 has reduced the supply of plankton. The murrelet decline is considered to be the immediate cause of the falcon decline.

It seems inconceivable that the Langara Peregrine Falcon population will regain its former numbers in the near future. If the murrelet decline continues, the Langara Island falcon population probably will dwindle further and, perhaps, vanish.

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