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IS NEST PREDATION BY STELLER'S JAYS *(CYANOCITTA STELLERI)* INCIDENTAL OR THE RESULT OF A SPECIALIZED SEARCH STRATEGY?

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Abstract -Decreased nest success and elevated levels of nest predation have been linked to changes in landscape configuration and increased edge. However, our current understanding of the mechanics of nest predation is limited. Using radiotelemetry and artificial nest experiments, we studied the ranging and nest-predation behavior of the Steller's Jay *(Cyanocitta stelleri)* in the managed forests of western Washington. Steller's Jays used a variety of forest seral stages, 95% of foraging observations occurred within 50 m of edges, and home range did not appear to be influenced by breeding success. Predation on artificial nests was elevated in high-use areas of home ranges, which suggests that Steller's Jays find nests incidentally while foraging for primary prey (insects). Steller's Jays did not appear to use a specialized search strategy to find nests, though they had a search image for nests and were capable of performing area-restricted searching for other food items (peanuts). To assess the risk of nest predation by Steller's Jays, it may be useful for managers to survey areas of concern for Steller's Jays and their foods. By equating relative abundance of Steller's Jays with nest predation risk, managers can then map predation risk onto the landscape of concern at the scale of the management unit.
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Key words: area-restricted search, *Cyanocitta stelleri*, diet, edge effect, foraging behavior, incidental predation, nest predation, search image, Stellar's Jay, Washington.

¿Es la Depredación de Nidos por *Cyanocitta stelleri* Incidental o es el Resultado de una Estrategia de Búsqueda Especializada?

RESUMEN. - Los niveles reducidos de éxito de nidificación y los niveles altos de depredación de nidos han sido relacionados con cambios en la configuracion del paisaje e incrementos en el area de bordes. Sin embargo, nuestro entendimiento actual de la mecánica de la depredación de nidos es limitado. Usando radiotelemetria y experimentos con nidos artificiales, estudiamos los movimientos y el comportamiento de depredación de nidos por parte del córvido *Cyanocitta stelleri* en los bosques manejados del oeste de Washington. Esta especie se encontró en una variedad de estadios sucesionales del bosque, el 95% de las observaciones de forrajeo tuvieron lugar a menos de 50 m de bordes y el area de hogar no pareció estar influenciada por el éxito reproductivo. La depredación de nidos artificiales fue elevada en los sectores del area de hogar con alta frecuencia de uso, lo que sugiere que los córvidos encuentran los nidos incidentalmente mientras forrajean en busca de sus presas principales (insectos). Estas aves no parecieron emplear una estrategia de búsqueda especializada para encontrar nidos, aunque tuvieron una imagen de búsqueda para nidos y fueron capaces de realizar búsquedas de otros items

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alimenticios (rnani) en un area restringida. Para establecer el riesgo de depredaci6n de nidos por parte de C *sielleri,* podria ser útil realizar censos de esta especie y sus alimentos. Considerando como equivalentes la abundancia relativa de C *stelleri* y el riesgo de depredaci6n de nidos, es posible mapear este riesgo sobre el paisaje de interés ala escala de la unidad de manejo.

DECLINES IN SONGBIRD populations resulting from decreased nest success are often linked to changes in configuration of natural land cover and increasing edge (Paton 1994, Andren 1995, Robinson et al. 1995). Fragmentation effects are frequently a complex combination of predator abundance and behavior and landscape configuration. Generally, nest predation levels are elevated in landscapes that include human settlement and recreation, but not in landscapes composed of a mixture of forest seral stages (Murcia 1995, Marzluff and Restani 1999, Chalfoun et al. 2002). Our understanding of mechanisms linking nest predation and landscape configuration, however, remains shallow (Marzluff et al. 2000). Specifically, we know very little about how nest predators locate nests and whether that process is influenced by landscape attributes (Paton 1994, Marzluff and Restani 1999, Chalfoun et al. 2002).

Nest predators may find nests incidentally while foraging for other foods or as a result of specialized search strategies. Incidental predation is "the fortuitous capture of an unexpected prey item, the consumption of which does not change the predator's foraging behavior" (Vickery et al. 1992:281). In that context, one species may be primarily responsible for nest predation events in an area, elevating nest predation levels upwards of 50%, despite the fact that nest contents are not the predator's primary food source (Vickery et al. 1992). In some systems, daily nest survival is reduced because of incidental predation by predators attracted to areas of high primary-prey abundance that coincide with areas used by nesting birds (Yanes and Suarez 1996). Modeling of incidental predation demonstrates that a single predator can find nearly a quarter of available nests in an area during the course of its daily movements, whereas multiple predators can elevate predation to 90% under the same circumstances (Lloyd et al. 2000). Thus, predators may have a profound effect on nest survival solely because of chance detection of nests.

In contrast, avian predators like corvids may use specialized search strategies, such as area-restricted searching, to find nests. Tinbergen et al. (1967) described area-restricted searching as an intensified search around the area where an initial prey item was found, restricted to the initial food type found, and documented such activity in Carrion Crows *(Corvus coronet)* searching in plots containing eggs in "crowded" versus "scattered" formations. Area-restricted searching continues until the predator fails to find a prey item within a threshold distance, or a "giving-up distance" (Croze 1970). American Crows (C *brachyrhynchos)* and Common Ravens (C *corax)* appear to use area-restricted searching to find nests of Pinyon Jays *(Gynmorhinus cyanocephalus;* Marzluff and Balda 1992). Several other studies have proposed area-restricted searching behavior, by a variety of predators, as a mechanism influencing nest predation (Hogstad 1995, Schmidt and Whelan 1998, Martin and Martin 2001).

The Steller's Jay *(Cyanocitta stelleri;* hereafter "jay") is a nest predator of concern in the Pacific Northwest, largely because of its potential effects on Neotropical songbirds and the threatened Marbled Murrelet *(Brachyramphus marmoratus;* Marzluff et al. 2000). Jays are omnivorous; they consume fruits, insects, various animal matter, human refuse, and nest contents (Greene et al. 1998). They do not appear to perform area-restricted searching for nests (Marzluff and Balda 1992), but are capable of foraging systematically for other foods (Slaby and Slaby 1977). In addition, they are important predators whose relative abundance is correlated with predation on artificial nests (Luginbuhl et al. 2001). Jays are particularly abundant in fragmented landscapes (Raphael et al. 2002), dominating a corvid community consisting of American crows, Common Ravens, and Gray Jays *(Perisoreus canadensis)* in such settings (Marzluff et al. 2000), and are among the nest predators consistently found at edges (Sieving and Willson 1998, Brand and George 2001, Masselink 2001, Marzluff et al. 2004). Thus, jays may be a key link between forest fragmentation and nesting success. Though their territorial behavior has been described (Brown 1964, Oberski and Wilson 1991), little has been published regarding this species' home range (Greene et al. 1998, Masselink 2001, Marzluff et al. 2004).

Understanding jays' ranging behavior and relating it to nest-finding ability is an important part of ascribing a mechanism to nest predation by this species. We examined the nest-predation behavior of jays along edges in the managed forest landscape of the Olympic Peninsula, Washington. We tested three hypotheses using detailed observations of free-ranging jays and experimental manipulation of foods, including artificial nests. Our first hypothesis was that, because fledglings require parental care and are less mobile than adults, jays that fledged young would initially be less mobile than those that were unsuccessful at fledging young and would therefore have smaller home ranges than jays that were not tending fledglings. Second, we hypothesized that nest predation by jays was incidental, predicting that nest predation levels would be elevated in high-use areas of jays' home ranges. Our third hypothesis was that, though capable of forming search images, jays do not perform area-restricted searching behavior for nests with eggs, though they may do so for other foods.

METHODS

Study area.- We studied jay foraging behavior on the western side of the Olympic Peninsula, near Forks, Washington (47°56'N, 124°23'W), and at one additional site 30 km east of Seattle, Washington (47°37'N, 122°20'W). Sites contained overstory trees 80-250 years old; were 0-5 km from human settlements, recreation areas, or both; and were embedded within a matrix of various coniferous-forest seral stages (clearcut to late-seral). We selected sites within landscapes containing abundant berry-producing shrubs, a characteristic consistent with abundant jays (Marzluff et al. 2000, Luginbuhl et al. 2001). Lying within the Western Hemlock *(Tsuga heterophylla)* zone, study sites were characterized by a mild maritime climate and high levels of precipitation (1,550-3,000 mm $year^{-1}$), with Douglas fir *(Pseudotsuga menziesii)* as a sub climax species often dominating logged areas, and with hardwoods *(Alnus rubra, Acer macrophyllum)* in riparian and disturbed areas (Franklin and Dyrness 1988).

Home-range estimation and breeding success.- We trapped jays from April to May of 2001 and 2002 using baited noose carpets and mist nets. Jay vocalizations broadcast through a megaphone attracted jays to trap sites. Captured birds were banded with unique combinations of colored leg bands and fitted with 4-g (3% of body weight) backpack-mounted radio-transmitters (Advanced Telemetry Systems, Isanti, Minnesota) (after Buehler et al. 1995). We detected no adverse effects of transmitters on jays (Withey et al. 2001). Jays were monitored from May through mid-September of the 2001 and 2002 field seasons to determine home ranges and high- and low-use areas within respective home ranges. We tracked jays one to five times a week and took one to five locations during each tracking session, spreading locations over a range of daylight hours and weather conditions throughout the breeding season. We attempted to obtain visual observations on radiotagged individuals; we recorded locations directly onto maps or photos of sites during tracking sessions and used a global positioning system (GPS) unit to record locations at remote sites.

We fitted 26 jays with radiotransmitters, Seven radiotagged individuals dispersed from their respective trap sites and were not found again. One jay removed its radio transmitter in mid-season. Three pairs of jays behaved as mated pairs or used nearly identical home ranges; for experimental purposes, we considered each pair as a single home range rather than two separate ones. That resulted in a total of 15 home ranges determined by radiotelemetry (4 in 2001, 11 in 2002) for use in experiments. We obtained 25-89 point locations during the breeding season for each bird to determine home-range size and resource use. Out of a total of 928 locations, 33% were based on visual observations, ranging from 17% to 56% for each bird; for 63% of locations, we were close enough to jays to detect changes in signal strength indicating either movement or stationary behavior without directly observing them. Only 3% of locations were determined solely by triangulation from two to four points within a study site. Spot-mapping and regular observation of untagged individuals at study sites produced an additional six areas in which to conduct experiments.

In addition to the 26 birds that we trapped and monitored in 2001-2002, we examined horne range and breeding success of 47 jays that had been monitored from 1995 to 1998 (Marzluff et al. 2004). Those jays were captured, radiotagged, and monitored using the same methods described above from March through mid-September. Each radio tagged bird in 1995-1998 and 2001-2002 was observed during only one breeding season.

We also attempted to determine the success of all radiotagged individuals at fledging young. We used the presence of fledged young in association with radiotagged individuals to indicate breeding success of the latter, because nests were rarely found. Fledglings were usually conspicuous on the horne range, because of their noisy begging and propensity to closely follow parents for a month or more. Of the total 73 radiotagged jays (26 from 2001-2002, 47 from 1995-1998), 39 were both adequately sampled for horne-range estimation (see below) and had confirmed breeding success status. Of those 39, 15 were never seen with fledglings, whereas 24 were observed with fledglings.

We used fixed kernel estimation with least-squares cross-validation (Kernohan et al. 2001) in the ANIMAL MOVEMENTS extension of ARCVIEW (ESRI, Redlands, California; Hooge and Eichenlaub 1997) to determine home ranges and high- and low-use areas within home ranges as estimated by utilization distributions (DDs). The UD, a probability density function (Silverman 1986) that quantified our radiotagged individuals' relative use of space (Kernohan et al. 2001), represents the probability of a jay occurring at each location within its horne range as a function of the relocation points we obtained (White and Garrott 1990). Following Seaman et al. (1999), we defined jays as adequately sampled if we obtained ≥30 locations. We obtained between 30 and 89 locations for 39 individuals. There was no positive correlation between number of locations and horne-range size of adequately sampled birds ($r = 0.15$, $P = 0.36$, $n = 39$; we used the minimum convex polygon [MCP] method of horne-range estimation to test that correlation, because it is the most sensitive to location sample size; Kernohan et al. 2001). We used the area (hectares) of the 95% contour of the UD as our estimate of horne-range size for all subsequent analyses, except to examine potential increase in horne-range size during the postfledging portion of the season (see below).

Experimental procedure to test for incidental predation, area-restricted searching behavior, and search-image formation.—In 2001-2002, we examined nest-predation behavior within the 15 horne ranges determined through radiotelemetry and the six additional spot-mapped areas. We used combinations of artificial nests, plastic dishes, Japanese Quail (*Coiurnix japonica;* hereafter *"Coturnix")* eggs, and peanuts to test for incidental predation, area-restricted search strategy, and search-image formation. Nests, constructed of straw and plastic adhesive, and plastic dishes, painted green, were roughly the same size (10-13.5 cm in diameter, 4-5 cm deep). In 2001, each artificial nest contained two *Coiurnix* eggs coated in paraffin to aid in predator identification (Fig. 1A). One egg was filled with ordinary household caulking adhesive, which dried to a solid but impressionable substrate, and attached by wire to the nest; this helped to ensure that at least one egg retained marks of a predation event. The other egg, though dipped in paraffin, retained its edible contents, ensuring that jays were rewarded for preying on nests. We made edible and plastic-filled eggs as similar looking as possible so that jays would not learn to distinguish between them by sight, and thus remove the edible egg without markirrg the plastic-filled egg. In 2002, we used nests and plastic dishes containing either one *Coturnix* egg, coated in paraffin and secured with cotton-polyester thread and superglue, or four peanuts (Fig. 1). We placed nondrying plasticine clay around the rim of the dishes containing peanuts to obtain foot or bill impressions (or both) of predators. *Coiurnix* eggs were well suited for the present study, because past studies have shown that small mammalian nest predators have difficulty handling them (Boag et al. 1984, Reitsma et al. 1990). That helped to minimize predation by other nest predators and thus kept as many predation opportunities open to jays as possible. We handled nests and plastic dishes with gloves and stored them in cedar chips to minimize human scent.

From mid-June through mid-September, we placed groups of nests or plastic dishes in the berry-producing shrub layer across all horne ranges. Nests or dishes within a group were standardized, to the extent possible, for relative height in the shrub and cover directly above and at 90° intervals, 1 m away from the nest (modified from Howlett and Stutchbury 1996;

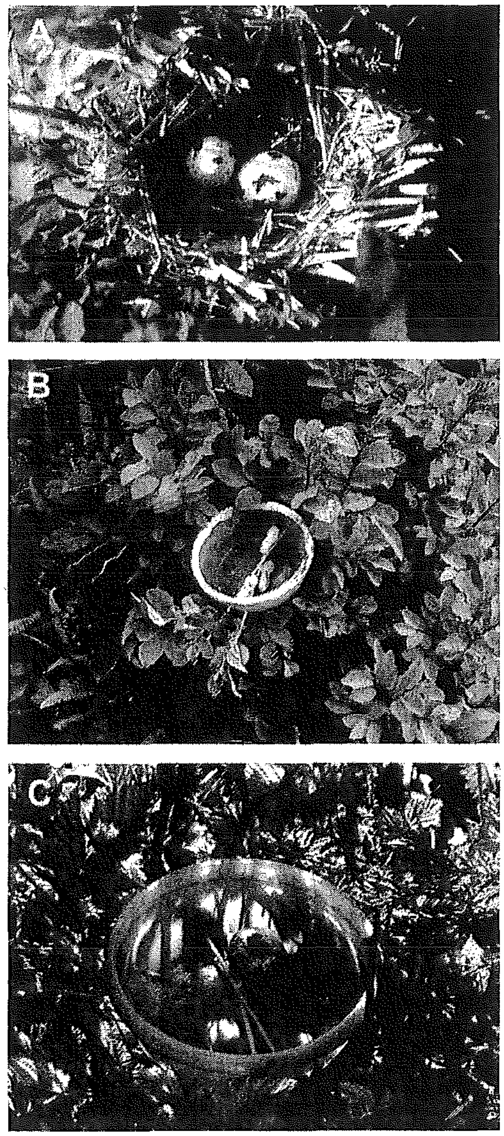

FIG. 1. Containers used in our experiments. (A) Artificial nests used in 2001 and 2002 to hold *Coturnix* eggs or peanuts. Note that the egg on the right was preyed on by a Steller's Jay. (B) Plastic dish containing peanuts, with nondrying plasticine clay around the rim to obtain foot or bill impressions (or both) of predators. (C) Plastic dish with *Coiurnix* egg tied to center.

mean ± SE differences between members of a group in 2001: 1.2 ± 0.5% overhead cover, 7.3 ± 0.8% side cover, n = 61; 14.2 ± 2.3 cm to top of shrub, n = 53; mean differences between members of a group in 2002: 0% overhead cover, 8.5 ± 0.5% side cover, 29 ± 3% ratio of distance from nest to top of shrub to distance of nest to bottom of shrub, n = 206). In 2001, nest height ranged from 30 to 200 cm above ground, with a mean of 68 ± 2.4 cm from the top of the shrub; in 2002, mean nest height above ground was 93 ± 2.4 ern, with a mean 49 ± 1.6 cm from the top of the shrub. We set up experiments during the day, noting any jay activity in the area. If birds flew in to observe us during the course of set-up, we removed the nests and waited for the birds to leave; or we returned the following day and set nests up in a slightly different location. Groups of nests were monitored daily for 12 days. If one member of a group was preyed on by jays (Fig. 1A), the remaining members of the group were monitored for a subsequent five days. If predation was determined to be by an unknown or nonjay predator; we replaced the nest or dish or the contents as needed, and the experiment continued for the allotted time. Throughout the season, three video cameras capable of recordingfor four consecutive hours were used among experiments to photographically document predation by jays and other predators.

A single experimental design allowed us to test the hypothesis that predation by jays is incidental and that jays do not perform area-restricted searches for nests (Fig. 2). To test for incidental predation, one pair of nests was set up in a high-use area of the home range, and one pair in a low-use area (Table 1). An area was designated as "high-use" if we regularly observed jays there, and berries were available; an area was considered "low-use" if jays were seldom observed, and berries were not presently available. On the basis of kernel density estimates for home ranges in 2001, high-use areas averaged 57 ± 9.7% use (n = 4) and low-use areas averaged 26 ± 6.0% use (n = 4). Location of pairs of nests followed changes in location of high- and low-use areas on jays' home ranges as the season progressed. To simultaneously test for an area-restricted search strategy, we placed pairs of nests different distances apart (1–4, 5–45, or 50-250 m) in both high- and low-use areas. Our logic was that nests close together would be more likely to be both destroyed if jays showed area-restricted searching behavior, whereas nest fate would be uncorrelated to the distance between nests if jays found nests

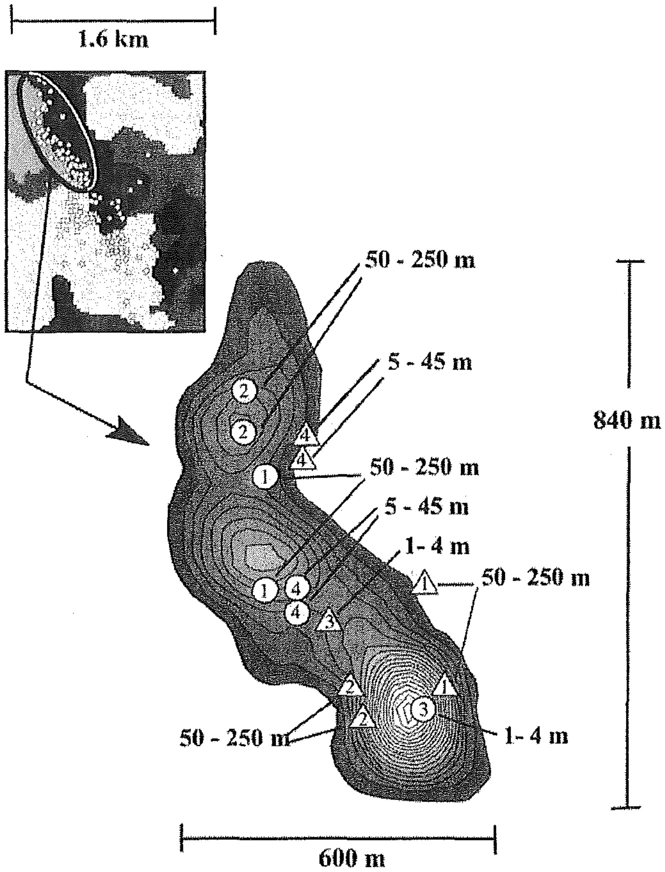

FIG. 2. One set-up design allowed us to test for incidental predation and area-restricted search strategy simultaneously in the 2001 field season. Inset: One study site composed of clearcut, early-, mid-, and late-seral forest patches (light to dark, respectively); location points (small dots) for three jays at this site observed during the breeding season; the circled portion indicates the locations used to estimate the home range of one individual.. Main frame: The 5-95% contours (light to dark, respectively) of the home range as estimated by the utilization distribution (UD); to test for incidental predation, a pair of nests was set up in a high-use area (circles), and a pair in a low-use area (triangles); to simultaneously test for area-restricted searching behavior, we placed members of a pair different distances apart; locations of experiments (1-4) followed the changes in location of high- and low-use areas on jays' home ranges as the season progressed; each home range had pairs of nests at each distance class, but only one distance class was presented per experiment.. This particular home range and the experiments placed within it are representative of the others used in the study.

randomly. Each home range had pairs of nests presented at each distance class, but only one class was presented at a time (i.e. two pairs of nests presented simultaneously in high- and low-use areas were always in the same distance class). To augment sample size in examining area-restricted searching behavior, we set up an additional 13 pairs of nests in only high-use areas (Table 1).

To test our hypothesis that, though capable of forming search images, jays do not perform area-restricted searching behavior for nests with eggs, though they may do so for other foods, we examined jay behavior toward four

TABLE 1. Summary of experimental designs used in 2001-2002. "Experiment type" refers to nest-predation behaviors tested for in Steller's Jays. "Container configuration" refers to number and placement within a home range of nests, plastic dishes, or both. We used both radiotelemetry and spot-mapping to determine home ranges for use in experiments.

			Home ranges used			
Experiment type	Year	Container configuration	Radio-telemetry	Spot-map	Total	Experimental set-ups
Incidental predation	2001	One pair in high-use area, one pair in low-use	4	2	6	25
Area-restricted search	2001, 2002	One pair in high-use area	6	4	10	38
Search image and area-restricted search	2002	One group of four in high-use area	11	2	13	27 [a]

[a] Though we set up 32 experiments, small mammals reduced the number available to jays by 5.

combinations of foods and containers: (1) nests containing eggs, (2) nests containing peanuts, (3) plastic dishes with eggs, and (4) plastic dishes with peanuts. We used plastic containers, objects novel to jays, to help discern what prompted search-image formation: (1) the food presented, (2) the container in which it was presented, or (3) a combination of the two. A set of four similarly stocked containers (nests or plastic dishes) were placed in the home range within close proximity to one another: no two containers of the set were >4 m or <1 m apart. Sets of containers were placed in high-use areas only (48 ± 6.9% use, n = 11), to maximize predation opportunities (Table 1). On the few occasions when berry-producing shrubs were not available in the high-use area for all four nests-containers, false azalea *(Menziesia ferruginea)* or salal *(Gaultheria shallon)* were used as a substrate. Small mammals, attracted by the scent of peanuts, made five of the experiments unavailable to jays; those experiments subtracted, jays in each home range were presented with 1.1 ± 0.26 and 1.0 ± 0.25 (n = 13) experiments offering them food in nests and plastic dishes, respectively. We randomly assigned the order in which food and container type were presented to jays, so that not all home ranges were first exposed to one container or food type at the same time.

Foraging observations.- To put nest predation into the context of the general jay diet, we obtained 265 detailed foraging observations on 19 radiotagged individuals from 2001 to 2002 and 26 other individuals from 1995 to 1998. We observed jays throughout the course of the breeding season and recorded prey items taken, substrate upon which prey was collected, habitat, and distance to the nearest edge. Habitat categories included: (1) late-seral (>70% crown closure of conifer, >10% crown closure in trees, >54 cm diameter at breast height [DBH], and <75% hardwood-shrub); (2) mid-seral (>70% crown closure of conifer, <10% crown closure in trees, >54 cm DBH, and <75% hardwood-shrub); (3) early-setal (>10% and <70% crown closure of conifer, and <75% hardwood-shrub); (4) clearcut (<10% crown closure of conifer or >75% hardwood-shrub); (5) recreational (campgrounds and picnic areas) and residential; (6) water-related areas (riparian areas, bogs, streams, lakes).

Statistical analyses.-Our home-range and fledging-success data were not normally distributed, so we used a Mann-Whitney U-test to examine differences in area (hectares) of varying contours (5-95%) of the UD between jays that were successful and those that were unsuccessful at fledging young. To examine the influence that late-season (and therefore postfledging) movements had on home-range sizes of successful and unsuccessful individuals, we used a Mann-Whitney U-test to compare the increases in MCP home-range size caused by including point locations gathered from mid-July through September. We compared the increases for home ranges in which there were ≥20 point locations obtained through mid-July with those for home ranges where those points comprised no less than 43% of the total point locations obtained for the home range over the entire season. Minimum convex polygon is most appropriate here because there were too few point locations to obtain an accurate estimate of horne range using kernel methods. A two-tailed asymptotic significance, with a = 0.05, was used, because of ties in the Mann-Whitney ranks.

The experimental unit for examining incidental predation was the horne range (*n* = 6). We used a repeated-measures ANOVA to compare the proportions of the 12-day period survived by nests in high- versus low-use areas. Because of the small number of horne ranges, the experimental unit for examining area-restricted searching behavior was a pair of nests in which at least one nest had been found by a jay (*n* = 25), rather than a home range. We analyzed pairs only in high-use areas because of the consistently high levels of predation in those areas. Among the three distance classes (1-4, 5–45, 50-250 m), we used a contingency table to compare proportions of nests found and not found within the five-day period subsequent to predation on the first member of the pairs. We then used a Kruskal-Wallis test to compare time to predation (in days) of the nearest neighbors among the three distance classes. To examine behavior and search strategy for combinations of foods and containers, the experimental unit was a set of four nests or containers (*n* = 27). We used a contingency table to compare numbers of experiments found and not found among the four treatments (nests containing eggs, nests containing peanuts, plastic dishes with eggs, plastic dishes with peanuts), as well as the number of experiments in which all four containers were found during the first predation attempt. We used the latter test to compare among the four treatments as well as lumped categories of those treatments (nest vs. plastic dishes, eggs vs. peanuts). We also used separate ť-tests to compare time to first predation events between container-type and food-type categories, respectively. For all contingency tables in which expected values were <5, a likelihood ratio was used instead of a chi-square value, and those tests were two-tailed. Means are presented ± SE.

RESULTS

Home-range estimation and breeding success.- Horne-range size for all jays, based on the 95% contour of the UD, averaged 57.7 ± 9.5 ha (*n* = 39). There was no significant difference in home-range size between 24 jays that were successful and 15 that were unsuccessful at fledging young (successful: 50.0 ± 9.6 ha; unsuccessful: 70.1 ± 19.3 ha; U = 155; *P* = 0.47). There was no difference in the amounts of area used by the two groups anywhere among the 5-90% contours of the UDs (Fig. 3). Late-season movements caused an increase in MCP home range in 17 of 24 horne ranges, and there was no significant difference in area-increase between successful and unsuccessful jays (successful: increase = 57.3 ± 41.5ha, *n* = 14; unsuccessful: increase = 15.4 ± 10.8 ha, *n* = 10; U = 63, *P* = 0.68).

Average size of horne ranges used in the 2001-2002 experiments was 36.6 ± 13.2 ha (*n* = 17, members of two pairs that were used as a single home range during experiments were separated for this average). All horne ranges encompassed two or more forest structural classes, ranging from clearcut to late-seral. In 2001, proportion of home range that was considered "high-use" (57% use or greater) was 12 ± 3.2% of the entire horne range (*n* = 4) and ranged in size from 1.3 to

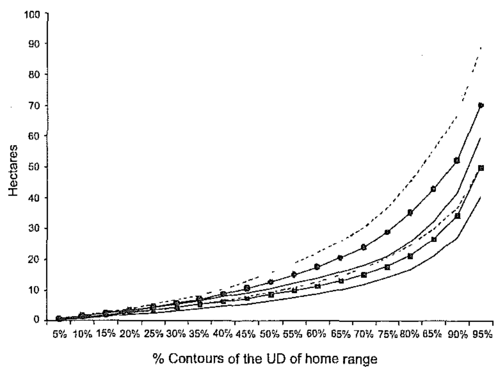

FIG. 3. No significant difference in overall home-range size (area of the 95% contour of the OO) and subsequent core-area size (the areas of the 5-90% contours) were evident between jays that were successful (*n* = 24) and unsuccessful (*n* = 15) at fledging young. Circles connected by a bold line indicate the mean for unsuccessful jays, and dashed lines indicate standard error (SE) for unsuccessful individuals. Squares connected by a bold line indicate the mean for successful jays, and thin lines indicate SE for successful individuals. The UD, a probability density function (Silverman 1986) that quantified our tagged individuals' relative use of space (Kernohan et al. 2001), represents the probability of a jay occurring at each location within its horne range as a function of the relocation points we obtained (White and Garrott 1990).

41.4 ha (12.3 ± 9.7 ha, n = 4). In 2002, proportion of the home range that was considered "high-use" (>48% use) was 15 ± 1.4% of the total home range (n = 11) and ranged in size from 0.3 to 9.6 ha (4.2 ± 1.0 ha, n = 11).

Incidental predation, area-restricted searching behavior, and search-image formation. - Jays found at least one nest in 25 of the 38 experiments set up to test for incidental predation and area-restricted searching behavior (experiments comparing high- and low-use areas and distance classes simultaneously, , n = 25; experiments comparing distance classes only, n = 13). Nests in high-use areas survived for fewer days than nests in low-use areas (Fig. 4). Nests in high-use areas survived 47 ± 10.0% (n = 6) of the 12-day period, or ~5.6 days. Nests in low-use areas survived 86 ± 5.5% (n = 6) of the 12-day period, or -10.3 days (F = 6.6, df = 1 and 8, P = 0.03, n = 5).

Discovery of neighboring nests was not affected by distance between nests. Overall, 48% of neighboring nests were found: four of eight nests 1-4 m apart, four of nine 5-45 m apart, and five of eight 50-250 m apart, with the likelihood of finding a neighboring nest independent of distance (likelihood ratio = 0.58, df = 2, P = 0.75). Of the 12 neighboring nests that were found, 6 were found on the same day as the first nest, 4 were found two days later, and 1 nest each was found on the third, fourth, and fifth days. Overall, it took jays the same amount of time (ranked from zero [found on the same day as the first nest] to six [not found within the 5-day period]) to find a neighboring nest, regardless of that nest's distance from the first nest (X^2 = 0.57, df = 2, P = 0.75, n_{1-4m} = 8, n_{5-45m} = 9, $n_{50-250m}$ = 8).

Jays found 20 of the 27 experiments used to test for search-image formation and area-restricted searching in the context of varying foods and containers. Of those available experiments, jays preyed on one or more members of a set of four nests or containers for all eight of the nest-egg sets, three of the six nest-peanut sets, four of the six container-eggs sets, and five of seven container-peanut sets. Although jays tended to prey on eggs in nests more frequently than on other combinations of foods and containers, the likelihood of a jay finding an experiment was statistically independent of treatment type (likelihood ratio = 6.6, df = 3, P = 0.09). Area-restricted searching, when jays found all four containers during the first predation attempt, was suggested in only 8 of 20 jay-depredated experiments. Jays found all containers in their first attempt in 6 of 8 experiments that presented jays with peanuts, and in 2 of 12 experiments that presented eggs. Thus, area-restricted searching was most evident when peanuts were presented, and least likely when eggs were presented (likelihood ratio = 7.1, df =

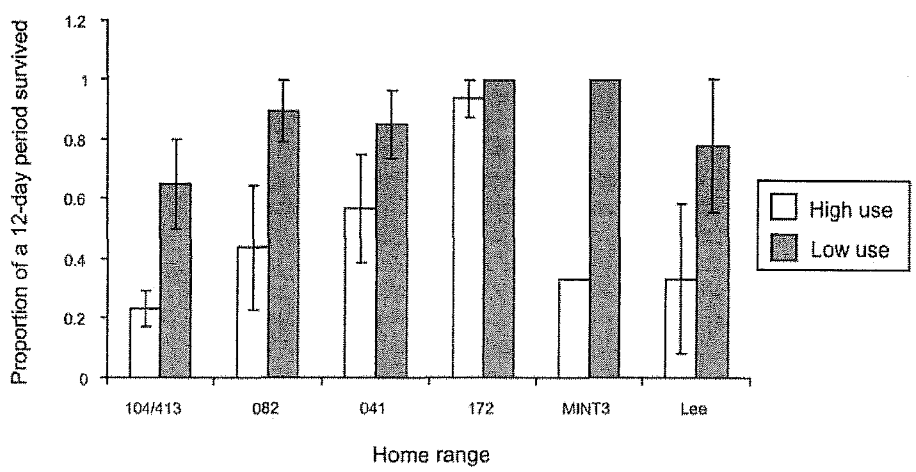

FIG. 4. Mean proportion (error bars indicate standard error [SE]) of a 12-day period survived by artificial nests among all home ranges. Nests in high-use areas survived for significantly less time than those in low-use areas. The experimental unit for predation in high- versus low-use areas of home ranges was the home range (n = 6).

1, P = 0.008). Despite finding all nest-egg experiments, jays were least likely to perform an area-restricted search upon finding eggs. However, jays were clearly attracted to nests. Jays found nest experiments twice as quickly as plastic dish experiments (nest: 2.7 ± 0.6 days, n = 11; plastic dish: 5.4 ± 0.8 days, n = 9; $t = -2.7$, P = 0.02), but simply finding a nest did not induce area-restricted searching behavior. Egg and peanut experiments were found in about the same amount of time (egg: 4.4 ± 0.9 days, n = 12; peanut: 3.3 ± 0.6 days, n = 8; $t = 1.1$, P = 0.29). The likelihood that jays would find all four containers of an experiment was independent of container type (likelihood ratio = 1.7, df = 1, P = 0.20), occurring in 3 of 11 experiments presented in nests and 5 of 9 presented in plastic dishes. Thus, it seems that while the container type dictated how quickly jays found an experiment, food type dictated whether or not jays used area-restricted searching.

Photographic conjirmaiion.- Video cameras documented predation by jays and mammalian predators on eight occasions. In 2001, jays were recorded preying on nests in high-use areas on two occasions. Though it was not photographed, we also observed in 2001 a jay family group perched within 2 m of a pair of nests 4 m apart, only one of which was subsequently preyed upon. At two nest-peanut experiment sites in 2002, Townsend's chipmunks (*Tamias toumsendiit*) were recorded removing peanuts from containers. We also documented jays preying on one nest-peanut experiment and one container-peanut experiment in two separate home ranges. Two nonpredation events, where a jay perched near or even made contact with plastic dishes containing eggs without preying on the contents, were photo documented in 2002 as well.

Foraging observations. - Jays consumed a variety of food items, primarily insects. Of 252 observations where prey items were identified, 84% were of insects, 12% fruits or seeds, and 4% human refuse. Jays foraged predominantly in trees (78% of 249 observations), but were also observed taking insects while in flight (6%), and foraging on the ground (6%), in shrubs (5%), and on human structures (3%). On only two occasions were jays observed using snags, and there was one observation of a jay stealing food from a Townsend's chipmunk. Almost half of all foraging observations were in mid- to late-seral forest (45% of 255 observations), and a quarter of all observations were in clearcuts and early-setal forest. Jays also used recreation and residential areas (14%), and areas closely tied to water (5%), such as riparian areas, cedar bogs, or on the ground at the edge of a water source. In 9% of observations, jays used both sides of an abrupt landscape edge, such as late-seral bordering early-seral or clearcut, or riparian areas bordering on clearcuts or early-seral forest. Jays gravitated toward edges in general: 63% of 206 foraging observations occurred within 20 m of an edge, 32% occurred between 21 and 50 m, 5% occurred between 101 and 200 m, and only one foraging observation occurred at >200 m from an edge.

DISCUSSION

At 57.7 ± 9.5 ha (*n* = 39), the average home range in our study was larger than the 24.6 ± 19.6 ha clearcut and 19.0 ± 20.9 ha forest-interior home ranges reported by Masselink (2001) for jays on Vancouver Island. Brown (1963) reported that jays maintained an "area of dominance" 120 m wide centered on the nest. If the area of dominance maintained by jays in our study area is of similar size, that corresponds to only the most heavily used 10% of the range covered by 50% of the successful jays (n = 24) and 60% of the unsuccessful jays (n = 15), or the most heavily used 20% of the range for 72% of all jays.

Unlike the home ranges of some raptors (Marzluff et al. 1997, Bloxton 2002), jays' home ranges did not seem to be influenced by breeding success. The lack of size difference between successful and unsuccessful home ranges may be attributable to the fact that all observed birds attempted to breed, and thus had nests up until the time of failure. However, we detected no significant difference in the increases in home-range size after all nests should have fledged (mid-July through September). Movements of birds tending fledglings did not appear to be any more restricted than those that did not have fledglings, and jays' nesting success should not affect the spatial extent of their nest-predation behavior.

The elevated levels of predation on artificial nests in high-use areas of jays' home ranges supports the hypothesis that jays prey on nests incidentally. Nests in high-use areas survived only half as long (5.6 days) as nests in low-use areas (10.3 days). Though we did not quantify the amount of "primary prey" available, we interpret high-use areas within home ranges to be representative of the overall richest food patches that jays are able to detect within their home range (Stephens and Krebs 1986). Our results are consistent with other studies that directly tested hypotheses about incidental predation (Vickery et al. 1992, Yanes and Suarez 1996, Schmidt et al. 2001), as well as those studies that, while not directly testing hypotheses regarding incidental predation, provided results that are consistent with nest predation as a random or incidental event (Angelstam 1986, Howlett and Stutchberry 1996, Yahner and Piergallini 1998).

Our results suggest that the density of nests placed in home ranges did not influence nest predation by jays, nor does it appear that jays performed an area-restricted search for nests with eggs. Nearest neighboring nests that were anywhere from 1 to 250 m away had the same likelihood of predation. In addition, of the four treatments offered to jays, nests with eggs were the least likely to suffer predation of all four containers during the first predation attempt: only one out of eight nest-egg experiments fit that criterion. Those results are consistent with previous research on jays (Marzluff and Balda 1992). In general, it appears that many nest predators do not rely on specialized search strategies to find nests, do not memorize nest locations (Yahner and Mahan 1999), and do not perform area-restricted searching behavior (Rangen et al. 2001). Interestingly, larger corvids (crows and ravens) appear to remember nest locations (Sonerud and Fjeld 1987) and use area-restricted searching to increase nest-finding efficiency (Marzluff and Balda 1992). Those corvids occupy much larger home ranges than jays and appear to actively look for prey (swinging their heads from side to side) as they fly above potential nesting areas. Flight may facilitate area-restricted searching, because large areas around known nests can be easily and effectively scanned. Efficient scanning may not be possible for jays, who frequently forage by spiraling up the branches of trees, apparently looking for insects as they hop or fly very short distances within and between trees.

Though it appears that jays forage incidentally for nests, that does not mean that they lack a search image for nests, or that they forage incidentally for all food items. Our study suggests that jays do have a search image for nests, as evidenced by the fact that (1) experiments that presented jays with nests were found more quickly than those that presented jays with novel items (plastic dishes) and (2) jays found all experiments that presented nests with eggs in 2002. Our study also suggests that jays forage systematically for peanuts, as evidenced by the fact that regardless of container type (nest or plastic dish), experiments that offered jays peanuts suffered predation of all four nests on the first predation attempt (indicative of area-restricted searching) 75% of the time. That ability is consistent with corvid behavior in general (Tinbergen et al. 1967, Croze 1970, Picozzi 1975, Angelstam 1986), and in previous work specifically related to jays (Slaby and Slaby 1977).

Many studies have documented density-dependent predation (Tinbergen et al. 1967; Dunn 1977; Hogstad 1983, 1995; Lariviere and Messier 1998; Martin and Martin 2001), and underlying assumptions of that phenomenon are area-restricted searching and search-image formation by nest predators (Lariviere and Messier 1998). Our results suggest that, though jays meet both of the criteria necessary for density-dependent predation to occur, the actual mechanism of nest predation by jays appears to be incidental encounter with readily recognized nests. Moderate-sized, generalist predators (e.g. corvids, raccoons *(Procyon lotor),* skunks [Mephitinae]) that are capable of noting varying patch quality across a landscape (on the scale of their home range) may not respond to increased nest density with area-restricted searching behavior when alternative food sources are abundant (Schmidt and Whelan 1999), and availability and location of alternative food sources has been shown to influence the functional response of nest predators (Schmidt and Whelan 1999). Jays are generalists that rely on seasonally abundant food sources, such as insects in the present study, and mast crops like acorns and pine seeds in other areas (Westcott 1969, Greene et al. 1998)-foods that are typically distributed in clumps across the landscape. Nests, by comparison, are likely to be evenly dispersed across a landscape. Jays may maximize foraging efficiency (Charnov 1976) by systematically searching for abundant foods and consuming nest contents opportunistically.

Our results suggest that incidental predators like jays can be important determinants of large-scale patterns of nesting success. For example, our finding that predation risk peaks in concert with space use by jays suggests a mechanism to explain elevated levels of nest predation along edges between forests and human settlements or recreation sites in our study area (Raphael et al. 2002). Jays may drive that effect, because they concentrate use along edges (Sieving and Willson 1998, Brand and George 2001, Masselink 2001, Marzluff et al. 2004), maintain home ranges that are not influenced by breeding success, and prey on nests incidentally. Thus, within a jay's home range, use and predation risk is expected to be greatest along edges throughout the nesting season. Further experiments that examine nest predation within areas of consistently high and low predator use or abundance would help elucidate the nuances of location-specific nest predation, such as that edge-effect.

Land managers concerned with the risk and potential effects of nest predation by incidental predators, such as jays, should document and map the relative use of areas by predators. Mapping relative use of areas by predators allows a manager to map the risk of nest predation onto any landscape of concern. This appears to be accurate within individual predators' home ranges because, regardless of breeding success, jays are most likely to prey on nests in the highest use areas of their home ranges. We suggest that this can be extended to larger scales more relevant to land mangers by surveying the relative abundance of jays across a landscape and equating the relative occurrence of jays to the risk of nest predation. Others have confirmed the general use of relating predator abundance to predation risk (Johnson et al. 1989, Andren 1992, Luginbuhl et al. 2001), but we are suggesting this be done in a spatially explicit, fine-scaled manner. Mapping the occurrence of suites of relevant predators (Johnson et al. 1989, Schmidt 1999, Marzluff et al. 2000) could be done to better anticipate areas on a landscape at greatest risk of nest predation. Combining a landscape perspective with detailed information about space use and nest-search strategies of multiple predators could provide managers with powerful tools to assess the risks and effects of nest predation.

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