erated from cells with inadequate sample sizes. No test was conducted on the Tule Lake NWR data because *t*-tests indicated the mean water-depth categories were not different. Bear River NWR and Lower Klamath NWR data sets revealed no difference in water-depth use by Western Grebe color morphs.

I also tested for differences in the proportion of each color morph at each water-depth zone (Miller 1981: 219). Of 15 cases tested, only 3 were significantly different: medium and high zones at Lower Klamath NWR and the low zone at Upper Klamath Lake.

The data support the hypothesis that light-phase Western Grebes feed farther from shore than dark-phase birds. However, the data are not totally consistent and, thus, this question warrants further study.

The data do not support the hypothesis that light-phase Western Grebes feed at greater water depth than dark-phase birds. However, the data must be viewed with caution due to several confounding factors: (1) water-depth categories were not directly related to distance categories; (2) 3 of 5 study areas were artificial water impoundments with relatively little change in water depth throughout the water basin (with the exception of "borrow ditches" adjacent to dike roads); and (3) the depth categories were only relative to other measurements on the same lake. Future research should concentrate on natural water basins to minimize these factors. Unfortunately, however, nearly all of the sympatric breeding populations in the U.S. are on artificial impoundments. One notable exception is Upper Klamath Lake.

A general hypothesis can be developed from these data. Most natural water basins have the shallowest water zones adjacent to shore, and water depth increases with approach to the approximate center of the basin. Light-phase birds may have evolved behavioral patterns closely associated with water depth. Use of a particular water-depth zone commonly may occur at a fairly consistent distance from shore. Thus, distance from shore may be an environmental "cue" regarding water depth and niche partitioning between the color morphs. Reduced niche overlap may limit competition for food resources, i.e. a "coexistence mechanism" (Cody 1974: 7). An alternative hypothesis is that niche partitioning is accomplished by spatial separation of near shore vs. farther from shore, and water depth and the evolution of "springing dives" are secondary to spatial factors. In either case, at artificial water impoundment areas where mean water depth is relatively similar (compared to natural water impoundments), distance from shore may influence spatial behavior of birds more than water depth.

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LITERATURE CITED

CODY, M. L. 1974. Competition and the structure of bird communities. Monographs in Population Biology No. 7. Princeton, New Jersey, Princeton Univ. Press.

GRINNELL, J. 1904. The origin and distribution of the Chestnut-backed Chickadee. Auk 21: 364–382.

MILLER, R. G. 1981. Simultaneous statistical inference, 2nd ed. New York, Springer-Verlag.

NUECHTERLEIN, G. L. 1981. Courtship behavior and reproductive isolation between Western Grebe color morphs. Auk 98: 335–349.

RATTI, J. T. 1979. Reproductive separation and isolating mechanisms between sympatric dark- and light-phase Western Grebes. Auk 96: 573–586.

———. 1981. Identification and distribution of Clark's Grebe. Western Birds 12: 41–46.

STORER, R. W. 1965. The color phases of the Western Grebe. Living Bird 4: 59–63.

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The Importance of Open Habitat to the Occurrence of Kleptoparasitism

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Direct competition among predatory birds for potential prey often is observed because of the large size of predator and prey, the often lengthy pursuit, and the open terrain in which many of these birds live. Such competition was brought to my attention vividly when I watched the interaction among four species of raptors over an open grassy prairie near Clewiston, Hendry County, Florida on 26 November 1961. A Merlin (*Falco columbarius*) flew rapidly over the prairie about 0.5 m above the ground and flushed two male Red-winged Blackbirds (*Agelaius phoeniceus*). It followed one blackbird closely until a male Northern Harrier (*Circus cyaneus*) rose from the prairie in front of them and struck at but missed the passing blackbird. The blackbird dropped to the ground and flew up again, and the Merlin forced it down a few meters farther on. The harrier caught up with them and captured the blackbird on the ground, where it rested with its prey as the Merlin flew away.

The harrier then flew up without the blackbird and landed a short distance away, and an adult Red-tailed Hawk (*Buteo jamaicensis*) landed on the blackbird a few seconds later. The harrier presumably saw the other hawk approaching and relinquished its prey. The Red-tailed Hawk rested on the ground for a few minutes, but then it also flew up with the blackbird as two Crested Caracaras (*Polyborus plancus*) arrived from a distant palm clump and began to dive at it. The Red-tailed Hawk was joined by another Red-tailed Hawk, possibly its mate, and they flew away with the blackbird, the caracaras in pursuit. The two hawks and the pair of caracaras repeatedly dived at one another in flight until the Red-tailed Hawk with the blackbird landed about 1 km from the capture site and the caracaras flew away. I had lost sight of the second Red-tailed Hawk, the harrier, and the Merlin by that time.

This interaction involved six raptors of four species for about 10 min. The first three species were vying for possession of the prey, but the caracaras may have been displaying interspecific territoriality (Newton 1979: 45) or aggression toward potential predators. Caracaras may nest during November in Florida (Kale 1978), and the catholic food habits of Red-tailed Hawks (Craighead and Craighead 1956) make them possible predators of nestlings. All of these raptors have been reported as kleptoparasites (Brockmann and Barnard 1979). Most reports of kleptoparasitism involve two species, but Bent (1938: 133) cited a report of a crow (*Corvus* sp.) taking a mouse from a Northern Harrier and losing it to a Crested Caracara.

The succession of interspecific interactions probably was determined by size, with the Red-tailed Hawk (1,220 g) dominant to the Northern Harrier (530 g), which was dominant to the Merlin (215 g; mean female weights from Newton 1979). Birds are not the primary prey of either Red-tailed Hawks or harriers (Craighead and Craighead 1956); therefore, pursuit by the Merlin and capture by the harrier made the blackbird more accessible to the larger species. The rapid reaction of the larger raptors indicates that avian predators are often aware of the activities of other predators.

Brockmann and Barnard (1979) enumerated six ecological conditions facilitating the evolution of kleptoparasitism: (1) large concentrations of hosts; (2) large quantities of food; (3) large, high-quality food items; (4) predictable food supply; (5) food visible; and (6) shortage of food. I believe their "food visible" condition is a consequence of another important condition, the openness of the habitat in which both the host and the parasite live. The openness condition has four effects: (1) potential and actual hosts can be watched, even continuously, at a longer distance; (2) capture and carrying of prey is visible for a longer distance; (3) hiding from kleptoparasites is difficult or impossible; and (4) prey items can be found easily after they are relinquished by the host. The following observations support each of these conclusions.

(1) Kleptoparasites can observe and follow hosts more easily in open habitats. African Fish Eagles (*Haliaeetus vocifer*) were important kleptoparasites on Goliath Herons (*Ardea goliath*, Mock and Mock 1980), and it may have been the eagles' ability to observe several hunting herons simultaneously that made food stealing a successful strategy (S. Carroll pers. comm.). In Washington I have observed most migrant Parasitic Jaegers (*Stercorarius parasiticus*) near flocks of their host species, Bonaparte's Gulls (*Larus philadelphia*) and Common Terns (*Sterna hirundo*). Laughing Gulls (*Larus atricilla*) and Heermann's Gulls (*Larus heermanni*) follow Brown Pelicans (*Pelecanus occidentalis*) as the pelicans forage and attempt to take prey from each successful pelican (Anthony 1906, Schnell et al. 1983). Similarly, I watched six Laughing Gulls follow two Great Egrets (*Casmerodius albus*) that were foraging on a sand flat in Florida. Although I did not observe the egrets capture prey, it seemed clear that the gulls were attending the egrets for possible kleptoparasitism.

(2) Kleptoparasites can observe prey capture and carrying more easily in open habitats. The Red-tailed Hawk that took the blackbird from the harrier (discussed above) was not visible to me when the interaction began and seemingly flew from a distance, perhaps beginning its approach as the Merlin chased the blackbird. Similarly, I have seen Parasitic Jaegers that were in cruising flight suddenly accelerate to harass a gull or tern with prey as far as 0.5 km away. Clearly, the visibility of prey is directly related to the openness of a specific habitat, an important variable to birds with long-distance vision.

(3) Hosts are less able to hide from kleptoparasites in open habitats. Furness (1978) found that Parasitic Jaegers were more successful in taking prey from a species of gull and a species of tern (33–44% of chases successful) than from three species of alcids that could dive to escape (11–21% successful). The ability of the host to "hide" was important in determining the success of these kleptoparasitic attempts. Similarly, Atlantic Puffins (*Fratercula arctica*) gave up their prey in 51% of kleptoparasitic attempts by Parasitic Jaegers when flying over land and only 22% of similar attempts when above the sea, where they could dive or descend to the surface (Andersson 1976). I rarely saw an intended host escape with its prey during many observations of Parasitic and Pomarine (*Stercorarius pomarinus*) jaegers kleptoparasitizing gulls and terns at sea. These birds can neither dive below the surface nor escape to the relative safety of a breeding colony. For the majority of these observations, only those birds that swallowed prey during the chase were able to retain it.

(4) Relinquished prey items can be found by kleptoparasites more easily in open habitats. Andersson (1976) observed that Parasitic Jaegers secured 15 of 18 items dropped by Atlantic Puffins. Although I have few recorded data, my impression after many years of watching jaegers with their many host species is that prey items dropped by hosts are rarely lost by jaegers. Most fish probably are disabled during the time it takes the parasite to force the host to drop them and are unlikely to escape the parasite. This is certainly true for a fish carried by a bird to feed its young.

Brockmann and Barnard (1979: 494) stated that "habitat as well as the behavior of the host may affect its chances of being parasitized," but they did not specify openness of habitat and overwater foraging as important considerations. Further, they suggested that "mixed colonies of fishing birds provide the ideal environment for kleptoparasitism with a plentiful supply of food items which are easily stolen" (Brockmann and Barnard 1979: 498) but did not mention that the major groups of marine kleptoparasites (frigatebirds, jaegers, and gulls) often display this behavior while away from these colonies. This is a reasonable oversight, because the best-known kleptoparasite, the Parasitic Jaeger, has been studied at seabird colonies in the north Atlantic rather than in the north Pacific, where it is a predator on its breeding grounds (Maher 1974) and a kleptoparasite at sea.

Although most seabirds use open habitats, raptors also can be used to test the hypothesis that openness of habitat is an important factor leading to kleptoparasitic behavior. The prediction is that raptors of open country are likely to be kleptoparasites while those of woodland are not. I used the list of kleptoparasitic raptors presented by Brockmann and Barnard (1979), with the addition of *Falco sparverius* as a kleptoparasite (S. Carroll pers. comm.), to test the hypothesis. The categorization is my own, based on extensive experience with all species on the list and information summarized by Brown and Amadon (1968). Of 22 North American falconiforms that forage primarily in open country, 10 (marked with asterisks) are known to be kleptoparasites: *Coragyps atratus, Cathartes aura**, *Gymnogyps californianus, Pandion haliaetus, Elanus caeruleus, Rostrhamus sociabilis, Ictinia mississippiensis, Haliaeetus leucocephalus**, *Circus cyaneus**, *Parabuteo unicinctus, Buteo swainsoni, B. albicaudatus, B. jamaicensis**, *B. regalis, B. lagopus**, *Aquila chrysaetos, Polyborus plancus**, *Falco sparverius**, *F. columbarius**, *F. peregrinus**, *F. rusticolus,* and *F. mexicanus**. However, none of the following 10 species, which forage primarily within forest and woodland in the same region, displays this behavior: *Elanoides forficatus, Accipiter striatus, A. cooperii, A. gentilis, Buteogallus anthracinus, Buteo nitidus, B. lineatus, B. platypterus, B. brachyurus,* and *B. albonotatus.* The difference between these two groups is significant (Fisher's exact test, $P = 0.01$).

I believe the observations presented here support what is an intuitively reasonable hypothesis, even though a bias is introduced by humans being able to detect kleptoparasitic interactions more easily in open terrain.

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LITERATURE CITED

ANDERSSON, M. 1976. Predation and kleptoparasitism by skuas in a Shetland seabird colony. Ibis 118: 208–217.

ANTHONY, A. W. 1906. Random notes on Pacific coast gulls. Auk 23: 129–137.

BENT, A. C. 1938. Life histories of North American birds of prey. Order Falconiformes (part 2). U.S. Natl. Mus. Bull. 170.

BROCKMANN, H. J., & C. J. BARNARD. 1979. Kleptoparasitism in birds. Anim. Behav. 27: 487–514.

BROWN, L., & D. AMADON. 1968. Eagles, hawks and falcons of the world. New York, McGraw-Hill.

CRAIGHEAD, J. J., & F. C. CRAIGHEAD, JR. 1956. Hawks, owls and wildlife. Harrisburg, Pennsylvania, Stackpole Co.

FURNESS, R. W. 1978. Kleptoparasitism by Great Skuas (*Catharacta skua* Brunn.) and Arctic Skuas (*Stercorarius parasiticus* L.) at a Shetland seabird colony. Anim. Behav. 26: 1167–1177.

KALE, H. W., II. (Ed.). 1978. Rare and endangered biota of Florida. Vol. 2, Birds. Tallahassee, Florida Game & Fresh Water Fish Comm.

MAHER, W. J. 1974. Ecology of Pomarine, Parasitic, and Long-tailed jaegers in northern Alaska. Pacific Coast Avifauna No. 37.

MOCK, D. W., & K. C. MOCK. 1980. Feeding behavior and ecology of the Goliath Heron. Auk 97: 433–448.

NEWTON, I. 1979. Population biology of raptors. Vermillion, South Dakota, Buteo Books.

SCHNELL, G. D., B. L. WOODS, & B. J. PLOGER. 1983. Brown Pelican foraging success and kleptoparasitism by Laughing Gulls. Auk 100: 636–644.

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