PATCH DYNAMICS OF THE BLACK-BELLIED WHISTLING DUCK

ZACHARY A. MAYER, JAMES A. MARLOW, AND PAMELA M. COLLINS

Faculty Editor: Rebecca E. Irwin

Abstract: We observed the spatial distribution of patches of the black-bellied whistling duck, *Dendrocygnus autumnalis*, at Palo Verde National Wildlife Refuge, Guanacaste Province, Costa Rica. Over a period of two days, we measured the spatial dispersion of patches on the entire marsh at one-hour intervals. We also measured the group size and local immigration and emigration rates of individuals in particular patches during 15 minute observations. In general, patch size and location were stable for larger patches of *D autumnalis*. Smaller groups changed more in size than larger groups, sometimes going extinct during the observation while other times growing by up to 50%. Conversely, larger groups were more consistent in size than smaller groups, growing only slightly during the observation period. The stability of patch locations and the size (relative and absolute) of larger patches may be important for future study concerning the spatial patterns of *D. autumnalis* in relation to resource and microhabitat dispersion.

Key Words: Dendrocygnus autumnalis*, Population ecology, Palo Verde*

INTRODUCTION

The concept of the metapopulation is important for understanding the distribution of organisms in fragmented resources patches. While each individual patch is distinct and isolated from the others, constant flow of individuals between patches creates metapopulation dynamics that are greater than the sum of interactions within each individual patch. Any population that is spatially distributed in patches and that maintains flow between patches can be thought of as a metapopulation (Krebs and Davies 1993). Such patchiness can even be observed on relatively small spatial scales, such as in communities of migratory birds on open water wetlands.

Some species of migratory waterfowl, such as the Black-Bellied Whistling Duck, *Dendrocygna autumnalis*, congregate in flocks of over a thousand individuals on open water habitats (James and Thompson 2001). The spatial distribution of these patches has been linked to biotic resources in the marshland they inhabit (E. González, *personal communication*). At the Palo Verde National Wildlife Refuge, the majority of the birds wintering on the marsh are *D. autumnalis*. While many of these *D. autumnalis* are year-round residents, the majority are migratory individuals from North America (M. Gómez, *personal communication*). *Dendrocygna autumnalis* break into small groups at night and fly away from their daily resting sites to feed; however, during

the day, they spend the majority of their time resting in large groups in open-water wetlands (Stiles and Skutch, 1989). Because *D. autumnalis* make up a large portion of the bird biomass on the marsh (M. Gómez, *personal communication*), they likely play an important role in the large interspecies flocks, and their spatial patterns may affect aquatic plant communities and nutrient cycling in the wetland (Mueller and van der Valk 2002).

We hypothesized that the distribution of *Dendrocygna autumnalis* on the open-water marsh in Palo Verde was a stable metapopulation, where the size larger patches does not change significantly over long time periods and never go extinct. To test our hypothesis, we analyzed the patches of *D. autumnalis* on the marsh. We predicted that (1) the net local immigration of *D. autumnalis* to a given patch would approximately equal the local emigration of *D. autumnalis* from that patch, regardless of patch size, and that (2) the size and location of the larger patches of *D. autumnalis* would remain constant within and between days.

METHODS

We conducted our study on 13 and 14 January, 2007, on a stretch of actively managed marsh along the Rio Tempisque directly in front of the Organization for Tropical Studies (OTS) research station in the Palo Verde National Wildlife Refuge, Guanacaste Province, Costa Rica. The actively managed regions of the marsh that we observed are periodically cleared of cattails. The cattail clearing creates shallow regions of open water with floating mat vegetation, which is preferred habitat for a wide variety of waterfowl, including *D. autumnalis* (Stiles and Skutch, 1989). *Dendrocygna autumnalis* distribute themselves throughout the marsh in dense, clearly defined clusters or patches, with few or no *D. autumnalis* occupying the space between patches.

To address our first prediction, that the net local immigration of *D. autumnalis* to a patch would approximately equal the net local emigration of *D. autumnalis* from that patch, two observers and a recorder were positioned atop a bird tower in front of the OTS station for three hours each morning and afternoon. Each observer selected a patch of *D. autumnalis*, estimated the number of individuals in that patch, and recorded every duck that flew into or out of the patch over 15 min. For each patch and observation period, we also recorded the time of day, location, microhabitat type (mud, shore, or floating mat vegetation), and whether the patch was disturbed by the passage of livestock

through it. To determine the relationship between initial patch size and net flux of *D. autumnalis* per 15 min observation period, we used a correlation analysis.

To address our second prediction, that the size and location of the larger patches of *D. autumnalis* would remain constant within and between days, we climbed to the Mirador Guayacán lookout behind the OTS station approximately 400 feet above the marsh. On two mornings at 0745, we took three sets of photographs of the entire marsh, each an hour apart and used Jasc Paint Shop Pro 8 to generate time-lapse maps of the distribution of duck patches on the marsh for both mornings. We also photographed one large patch in 15 min intervals over 150 min, starting at 0755, to document the changes of one large patch over two days.

RESULTS

We found a significant positive correlation between the initial patch size (natural-log transformed) and net change in the number of *D. autumnalis* ($r = 0.57$, $n = 24$, $p = 0.0033$; Fig. 1). Larger patches of D. *autumnalis* tended to have a net local immigration of *D. autumnalis*, while smaller patches tended to have a smaller local immigration, or even a local emigration, of *D. autumnalis*.

To calculate how volatile patches were, we took the absolute value of the percent change in the number of *D. autumnalis* over 15 minutes. We found a strong, negative correlation between the initial patch size (natural-log transformed) and the absolute value of the percent change in number of individuals (natural-log transformed) over 15 minutes in that patch. ($r = -0.55$, $n = 24$, $p = 0.0055$; Fig. 2). As patch size increased, the patches were less likely to change significantly; the larger patches are more stable.

Over the course of two days, the distribution of large patches of *D. autumnalis* over the entire marsh did not noticeably change (Fig. 3). The largest, most visible patches of *D. autumnalis* were in the same locations on both days.

We also found that a single large patch of *D. autumnalis* did not go extinct after 150 minutes starting at 8 AM, even after disturbance by a horse (Fig. 4). After disturbance, the patch quickly regained its original shape, with a slightly lower density (Fig. 4, panels 1 and 10).

DISCUSSION

Fragmented populations connected by local immigration and emigration between patches can be thought of as one metapopulation (Krebs and Davies 1993). These patches can exist at equilibrium, where the immigration rate approximately equals the emigration

rate from each patch, or they can be sources or sinks, where either immigration or emigration

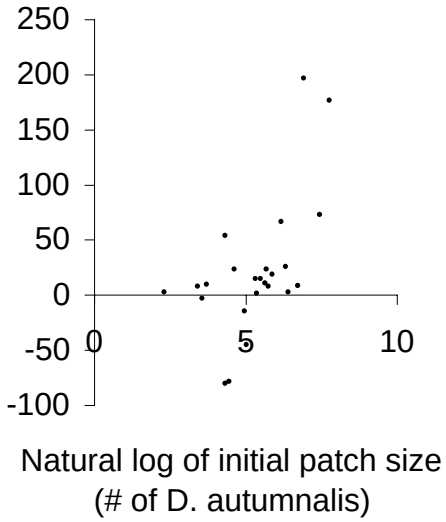

Figure 1. Relationship between initial patch size and net change in number of *Dendrocygnus autumnalis* individuals, as observed over 15 min intervals. Larger patches tended to have a larger local immigration of *D. autumnnalis* than smaller patches.

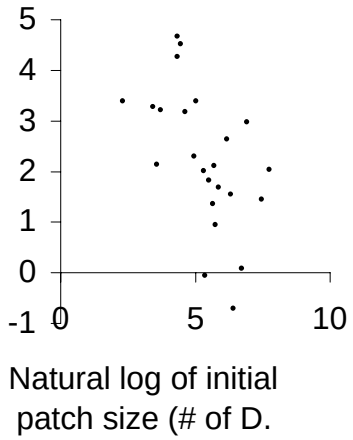

Figure 2. Relationship between initial patch size and percent change in number of *Dendrocygnus autumnalis* individuals, as observed over 15 min intervals. Smaller patches varied more in their percent changes, while larger patches consistently had a small, positive percent change.

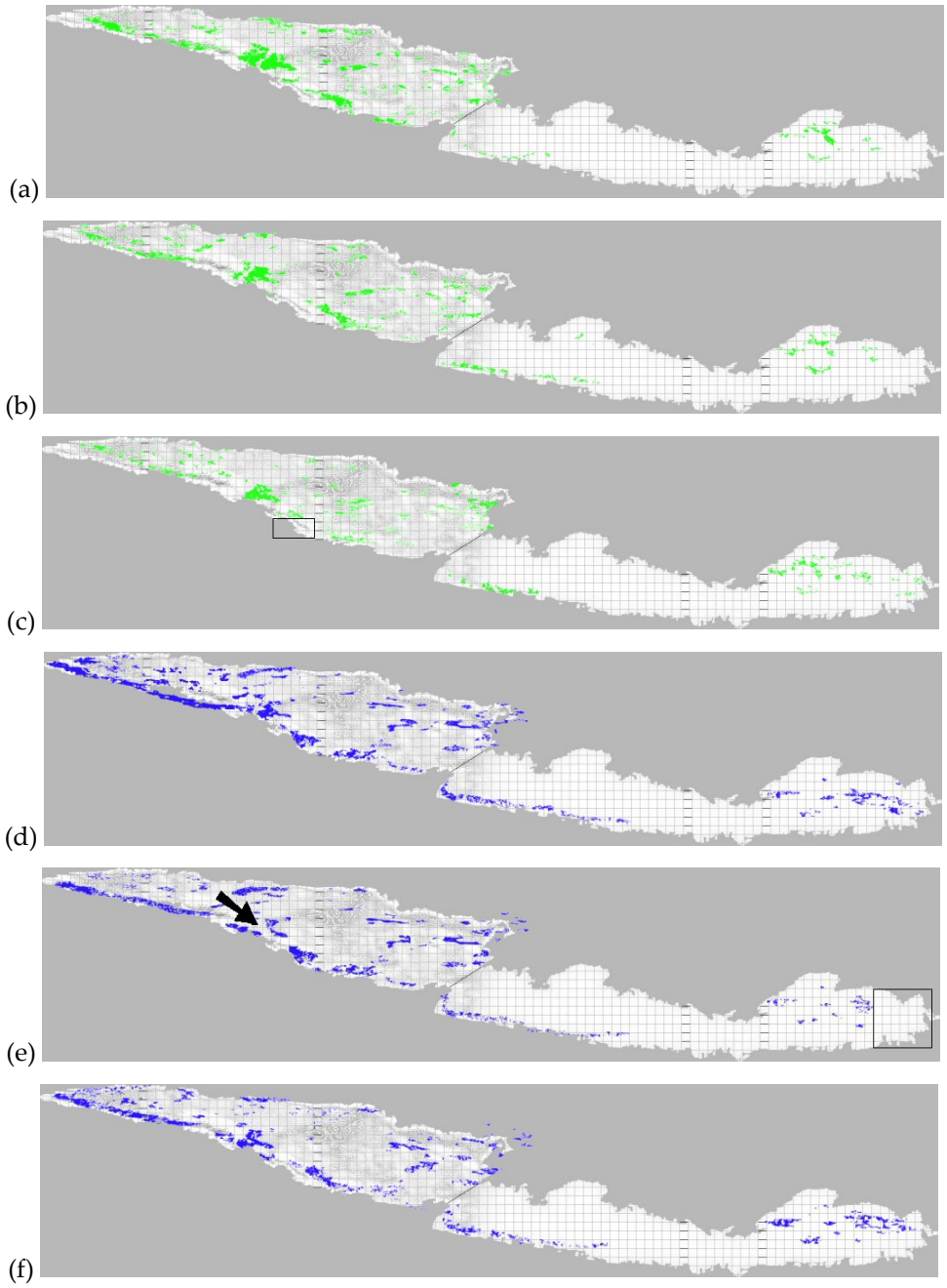

Figure 3. Maps of *Dendrocygnus autumnalis* patch distributions in the marsh on the mornings of 12 and 13 January, 2007. Green areas represent duck patches on Day 1, while blue areas represent patches on Day 2. The black boxes are areas for which there is no data. Maps were constructed from photos taken at (a) 0740 on 12 January, 2007, (b) 0840, (c) 0940, (d) 0745 on 13 January, 2007, (e) 0845, and (f) 0945. The black arrow in (e) shows the location of a disturbance caused by a grazing horse at 0840, which displaced a large number of *D. autumnalis*. Over the course of both days, the locations of the major patches of *D. autumnalis* did not change significantly.

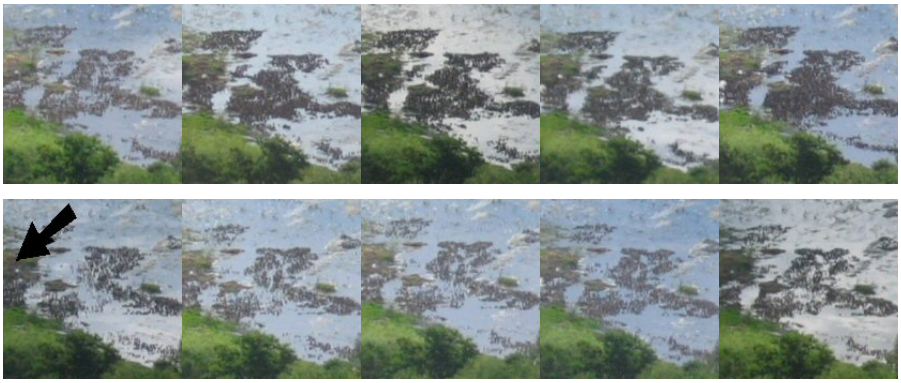

Figure 4. Time lapse photographs of a single large patch of black-bellied *Dendrocygnus autumnalis* on 13 January, 2007. Photographs were taken every 15 min and the first photograph was taken at 0755. The black arrow points to the source of a disturbance caused by a horse at 0840. Note that the shape of the patch does not change, while the size recovers after disturbance.

outweighs the other (Krebs and Davies 1993). Patches within a metapopulation often occur on patches of resources valuable to a specific species (1993).

A metapopulation can be found in any population that is spatially distributed in patches and that maintains some flow of individuals between patches. Such a distribution can be observed in the way *Dendrocygnus autumnalis* are spatially distributed across the marsh in Palo Verde, Costa Rica. This metapopulation is characterized by large, stable aggregations of *D. autumnalis*, interspersed with smaller, more volatile patches. The large patches of *D. autumnalis* are isolated by stretches of empty water, but there is frequent exchange of individuals between patches. Because the larger patches tend to grow in size, there appears to be a stable, long-term distribution of the larger patches of *D. autumnalis* in the marsh.

We found that larger patches of *D. autumnalis* tended to have a greater rate of immigration than emigration, while smaller patches had a net loss of individuals (Fig. 1). *Dendrocygnus autumnalis'* preference for larger patches is indirectly supported by the significant positive correlation we observed between initial patch size and the net change in number of individuals over a 15-min observation period, contradicting our first prediction, that the net inflow of ducks into a patch would equal the outflow of ducks from that patch, regardless of patch size. This behavior tends to create large, stable patches of *D. autumnalis* (Fig. 3); larger patches attract more individuals. While this prediction was disproven, it does not

necessarily mean that the ducks do not exist in a metapopulation. The larger patches may act as population sinks, but the percent change in patch size over the observation period averaged 1-2% of the total patch size.

Our results support our second prediction that the size and dispersion of major patches would not change greatly over time. We found that large patches of *D. autumnalis* tended to grow by a small amount over the observation period. The static location of these major patches as well as the observed immigration and emigration from patches provide partial support of our hypothesis that *D. autumnalis* exist in a metapopulation.

Large daily groups may also be important for predator defense, and larger groups may therefore be stable due to the dilution of individuals (Kornet et. al., 1992). Previous studies have suggested that large flocks of birds are better able to detect predators (Kornet et. al., 1992); *D. autumnalis* rapidly took flight in huge numbers in response to disturbance. Because larger flocks provide better protection against predators (Kornet et. al, 1992), it is logical that individual *D. autumnalis* would join larger patches on the marsh, which would tend to create large, stable patches of *D. autumnalis*. This hypothesis warrants further experimental investigation. Our observations of the flocks of *D. autumnalis* show that the largest, most visible patches of *D. autumnalis* are stable throughout the day, as well as between days, providing support for our second prediction, that the patches are stable throughout and between days. Our observations show very little change in the over-all distribution and size of large patches throughout the marsh. Even after significant disturbance, the largest patches of *D. autumnalis* quickly reformed, adding further evidence to support the idea that the *D. autumnalis* form large, stable flocks.

To further evaluate the patch dynamics of *D. autumnalis*, it would be informative to test whether an individual duck will pick a larger or smaller patch, when presented with the option. We would also like to further evaluate emigration from large patches, to test whether this behavior is due to random chance, or if individuals will leave dense patches in search of less dense ones. Finally, it would be informative to determine whether certain factors, such as the location of food resources, can be used to predict where a large patch of *D. autumnalis* is located. Because metapolulations are often distributed according to resource patches, correlation patches of *D. autumnalis* in the marsh at Palo Verde with the location of food resources would strongly support the hypothesis that the *D. autumnalis* community is a metapopulation.

LITERATURE CITED

Emlen, J. M. 1984. Pp. 385-388, 394 in Population Biology: The Coevolution of Population Dynamics and Behavior. Macmillan Publishing Company: New York.

Hartshorn, G. S. 1989. Palo Verde. Pp. 127-132 in D. H. Janzen, editor. Costa Rican Natural History. University of Chicago Press: Chicago, IL.

James, J. D., and J. E. Thompson. 2001. Black-bellied Whistling-Duck (*Dendrocygna autumnalis*). *In* The Birds of North America, No. 578 (A. Poole and F. Gill, eds.). The Birds of North America, Inc., Philadelphia, PA. http://bna.birds.cornell.edu/BNA/account/Black-bellied_Whistling-Duck/BEHAVIOR.html, accessed 1/21/07.

Kornet, D. B., E. S. McLanahan, L. M. Mizak, C. R. Pruess. 1992. Vigilance and predator response distance in Black-Bellied Whistling D. autumnalis. Dartmouth Studies in Tropical Ecology, pp. 29-31.

Krebs, J. R. and N. B. Davies. 1981. Pp. 106-110 in An Introduction to Behavior Ecology, 3rd ed. Blackwell Science, Inc.: Cambridge, MA.

Mueller, M.H. and A. G. van der Valk. 2002. The potential role of D. autumnalis in wetland seed dispersal. *Wetlands* 22: 170-178.