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THE POTENTIAL ROLE OF HURRICANES IN THE CREATION AND MAINTENANCE OF KIRTLAND'S WARBLER WINTER HABITAT IN THE BAHAMIAN ARCHIPELAGO

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ABSTRACT

The threatened migratory Kirtland's Warbler (KW, *Dendorica kirtlandii*) breeds exclusively in Michigan and overwinters nearly exclusively in the Bahamas Archipelago, where little is known of its winter habitat. Previous observations and our own studies indicate that KWs routinely use early successional or regenerating shrubby habitats on Eleuthera. Our preliminary results suggest that wintering KWs readily shift locations on Eleuthera as they track food abundance (especially fruit) that waxes and wanes at different sites as the winter proceeds. The use of disturbed sites and a pattern of winter movements that allows opportunistic use of the richest available food patches are consistent with a disturbance-adapted foraging strategy. Although all of our KW capture sites (N = 77) on Eleuthera show evidence of previous human disturbance resulting from agriculture or building construction, we hypothesize that the early seral stages of secondary broadleaf (coppice) habitats used by the warbler could also be produced by hurricanes. By reducing or eliminating canopy of tall coppice, hurricanes stimulate understory growth, which favors regeneration and colonization by fruiting shrubs. Moreover, hurricane storm surges in low-lying coastal areas may create patches for colonization by early successional plant species, some of which may be used by KWs. In addition, hurricanes may prolong the "life" of existing KW sites by setting back or delaying succession or regeneration. New growth after hurricanes may also result in increased abundance of arthropods and fruits consumed by KWs.

Hurricanes occur with sufficient frequency in the archipelago to be an integral part of the natural disturbance regime and were likely an important natural disturbance factor in presettlement times. However, no studies of KWs have yet been conducted in sites severely damaged by hurricanes. Therefore, this hypothesis remains to be tested, especially because of its conservation importance for understanding how KW winter habitats are produced.

INTRODUCTION

The Kirtland's Warbler (*Dendroica kirtlandii,* henceforth KW) is notable for its limited geographic distribution, which includes breeding grounds confined essentially to the state of Michigan, U.S.A., and wintering grounds restricted to the Bahamas Archipelago (both The Bahamas and Turks and Caicos Islands, henceforth The Bahamas). This songbird is one of North America's rarest bird species and has been the focus of intensive conservation efforts on the Michigan breeding grounds, which have successfully brought the population from a low count of 167 males in 1987 (Weinrich, 1988) to a high of 1,418 males in 2005 (KW Recovery Team, unpubl. data). So far, the success of this recovery effort has been attributed largely to the control of brood parasitism by Brown-headed Cowbirds (*Molothrus ater*) and management of fire-dependent Jack Pine (*Pinus banksiana*) to ensure that adequate breeding habitat is available in Michigan.

In contrast to the intensive research and management efforts for the KW on the Michigan breeding grounds (e.g., Huber, 1982; Probst, 1986; Kepler *et al.*, 1996), relatively little is known of the species' biology and habitat use on the wintering grounds where it spends over seven months of the year. Recent studies indicate that wintering ground events can affect migrant populations (Rappole *et al.*, 1989; Robbins *et al.*, 1989; Sherry & Holmes, 1995; Marra *et al.*, 1998; Sillett *et al.*, 2000) and the absence of wintering ground information and conservation efforts could compromise KW breeding ground conservation efforts.

Although KWs have been difficult to find in The Bahamas, observers have concluded that winter habitat consists primarily of low broadleaf scrub or low coppice (Challinor, 1962; Mayfield, 1972, 1992, 1996; Radabaugh, 1974; Sykes & Clench, 1998; Wunderle, Currie, and Ewert, unpubl. data). The importance of broadleaf scrub as KW winter habitat was emphasized by Mayfield (1996), who thought the warbler avoided Caribbean pine (*Pinus caribaea*) woodlands, despite structural traits of the pine woodlands that resembled those of the Michigan breeding grounds (Radabaugh, 1974). In contrast, analyses of winter reports of individual KWs and their own surveys led Lee *et al.* (1997) and Haney *et al.* (1998) to conclude that pine habitats, not broadleaf scrub, were a major wintering habitat.

Pine woodlands of The Bahamas may attract wintering KWs because of the shrubby broadleaf understory in which the warblers forage and not because of the pine trees *per se*, which are rarely used by the KWs (Lee *et al.*, 1997; Haney *et al.*, 1998). Caribbean pine woodlands, because of their susceptibility to fires, may provide the early shrubby seral stages used by KWs. Lee *et al.* (1997) and Haney *et al.* (1998) recognized that wintering KWs also use regenerating scrub in the absence of pine; they argued such habitats are a result of recent human disturbance and do not represent the original natural habitat before humans arrived in the archipelago. Thus, they attributed the presence of KWs on islands without pine to anthropogenic habitat disturbance of recent origin. Therefore, a major issue of contention is whether the KW's winter habitat most commonly results from anthropogenic effects (e.g., abandoned farmland) or from natural disturbances, such as hurricanes, or the natural fires that have maintained Bahamian pine ecosystems well before human occupation (Byrne, 1980).

By emphasizing the importance of natural fires for producing early successional scrub habitats in pine woodlands, Lee *et al.* (1997) and Haney *et al.* (1998) were the first to address the question of how the early successional habitats frequently used by wintering KWs were naturally produced in The Bahamas before human settlement. Lee *et al.* (1997) only briefly mentioned the possibility that hurricanes might also produce winter habitat suitable for KWs.

In this paper, we elaborate on the importance of hurricanes as natural disturbance factors by reviewing the characteristics of hurricanes and their effects on vegetation, which have the potential to produce KW habitat by creating or maintaining early successional patches of broadleaf vegetation. We relate this review to observations, including our own, of the winter ecology of the KW. Based on these observations and our review of the literature, we hypothesize that hurricanes occur with sufficient strength and frequency in The Bahamas to be an integral part of the natural disturbance regime responsible for setting back succession and producing KW winter habitat. Hurricanes may complement fire as a natural disturbance factor in the pine islands and may be the dominant natural disturbance factor on islands without pines where hurricanes may now complement anthropogenic production of disturbed habitats. Understanding how KW winter habitat is naturally produced is of fundamental conservation importance for both protection and management of KW habitat on the wintering grounds.

KIRTLAND'S WARBLER AS A DISTURBANCE-ADAPTED SPECIES ON THE WINTERING GROUND

The KW is a disturbance-adapted species on the breeding grounds, as evident in its restriction to fire-dependent jack pine stands of 6-21 years of age in Michigan (Mayfield, 1992). Accordingly, it should not be surprising that the warbler also uses disturbed habitats on the wintering grounds. Evidence is accumulating, from the work of others and our ongoing work on Eleuthera, which indicates that KWs are also disturbance-adapted species on the wintering grounds. For example, all of our KW captures (N = 77) on Eleuthera occurred in second growth coppice sites, which showed evidence of previous human disturbance such as abandoned agricultural lands (primarily ground crops or citrus plantations) or abandoned building sites. These capture sites ranged in age from 5 to 27 years after abandonment for the few sites for which we know the age of abandonment. Vegetation height was relatively low at 60 KW capture sites, where the mean canopy height was 3.3 m $\pm$ 1.4 SD and the modal foliage height class occurred at 0.5–1.0 m in foliage profiles measured in 0.03 ha plots at each capture site (see habitat methods in Currie *et al.*, 2005). This contrasts with the mean canopy height of 11.9 m $\pm$ 2.2 SD and modal foliage height class at 6–8 m in two 0.03 ha plots in tall coppice on Eleuthera (Currie *et al.*, 2005). Thus, our observations are consistent with previous observations (Lee *et al.*, 1997) that KWs are found in shrubby or scrubby disturbed sites of relatively low (broadleaf) stature and are absent from tall coppice.

Despite controversy over KW winter habitat use at the ecosystem level, there appears to be agreement that the wintering warbler forages for insects and fruit close to the ground (0-3 m) and uses sites characterized by low broadleaf scrub/shrubs of varied foliage layers (with or without pine overstory) with small openings distributed throughout the vegetation, which may include some bare ground (Haney *et al.*, 1998; Sykes & Clench, 1998; Wunderle, Currie, and Ewert, unpubl. obs.). A variety of small fruits are consumed, but the fruits of several early- to mid-successional shrub species, such as wild sage (*Lantana involucrata* and *L. bahamensis*), West Indian snowberry (*Chiococca alba*), and black torch (*Erithalis fruticosa*), appear to be especially important (Sykes & Clench, 1998; Wunderle, Currie, and Ewert, unpubl obs).

Our preliminary results indicate that KWs may shift locations in the course of a winter as they track food resources, especially fruit. At sites where fruit abundance decreases during the course of a winter, we have observed a corresponding decrease in the number of KWs. In contrast, at a site where fruit abundance increased during the winter, we found a corresponding increase in the number of KWs during the winter. We have also observed color-banded individuals shifting 2.6 to 6.0 km between sites within a winter. Some KWs cover a considerable amount of area during the winter, as indicated by mean 95% adaptive kernel home range of 21.2 ha $\pm$ 23.3 SD for 13 radio-tagged KWs, each followed for approximately 21 days. Both observations of color-banded individuals and our telemetry studies indicate that KW winter home ranges (i.e., 95% adaptive kernel) overlap considerably and are not areas of exclusive use, although core areas (i.e., 50% adaptive kernels) often are areas of exclusive use. Nonetheless, overlap of core areas may be substantial in the few remaining patches with high fruit abundance when fruit abundance declines in neighboring areas in late winter.

These observations are consistent with the likelihood that wintering KWs are opportunistic in their use of habitat patches and that they will move among patches, if necessary, to track food abundance. Therefore, winter movement patterns indicate a flexible and opportunistic response to variation in winter food resources, as expected for a species that relies on disturbed habitat patches in which resources vary in both space and time.

HURRICANES AND BIRDS

In the Caribbean, tropical cyclones or hurricanes occur with sufficient frequency to be important factors in determining the structure and composition of ecological communities (Wadsworth & Englerth, 1959; Odum, 1970; Walker *et al.*, 1991). Hurricanes affect the biota of these communities both directly and indirectly, the indirect effects having the most substantial and longest lasting impacts (reviewed in Walker *et al.*, 1991; Wiley & Wunderle, 1994). Direct effects cause mortality due to exposure to storm winds, rains, and floods. Indirect effects occur mostly in the storm's aftermath and include loss of food supplies or foraging substrates, as well as loss of cover for hiding, roosting, or nesting. Animals respond in the short-term to these effects by changing their diet or shifting to less damaged locations, habitats, or sites within a habitat. Finally, hurricanes can set back plant succession creating a mosaic of habitat patches at different successional stages.

Hurricanes may directly cause some mortality of KWs during migration and on the wintering grounds, but it has not been demonstrated (Mayfield, 1992). Previous studies indicate that for most terrestrial forest birds, the greatest population effects of hurricanes occur in the aftermath rather than during the impact (Wiley & Wunderle, 1994). We suspect that most KWs on the wintering grounds in The Bahamas can survive the direct impact of hurricanes by dropping to the ground or into sinkholes and remaining immobile, except for dodging the occasional falling branch or tree trunk, as observed in other passerines during hurricanes (Wunderle, unpubl. obs). However, immediately after the storm, KWs may be stressed in the absence of food or cover. Although populations of frugivores, seedeaters, and nectarivores are most affected by hurricanes relative to insectivores (Wiley & Wunderle, 1994), it is unknown how KWs respond given a winter diet of fruit and insects. However, due to the tendency of KWs to abandon sites as fruit abundance declines and to shift to other sites with abundant fruit within the same winter (Wunderle, Currie, and Ewert, unpubl. obs.), we expect that KWs would readily shift from heavily damaged sites to less damaged sites with more food. Such location shifts are typical of the post-hurricane response of many frugivores (Wiley & Wunderle, 1994) and we would expect KWs to shift locations within and possibly between nearby islands in the archipelago as an immediate post-hurricane response, which would likely limit post-hurricane mortality. More importantly, in the longer term (2-15 years?), these storms undoubtedly play a beneficial role by producing regenerating habitat patches used by wintering KWs.

HURRICANES IN THE BAHAMAS

The Bahamas Archipelago lies within a region of the North Atlantic that is especially susceptible to hurricanes as they enter or exit the Caribbean basin and the North Atlantic Ocean. For example, in the period of 1899 to 1989, there was a total of 66 hurricanes, or a hurricane every 1.4 years, that crossed the waters of the archipelago (Shaklee, 1991; cited in Shaklee, 1996). However, the frequency of hurricane strikes on any particular island in the archipelago varies with several factors, including the position in the island chain, size of the island, and island orientation (Shaklee, 1996). The northern islands in the chain have a higher frequency of strikes than the southern islands due to the characteristic hurricane tracks in the region. Large islands are more likely to be directly hit than are small islands and islands that are oriented in an east-west axis are struck less frequently than islands oriented along a north-south axis. Estimates of hurricane strike frequencies for specific islands have been provided by various authors. For instance, for the period of 1886 to 1992, the island of Eleuthera had 55 hurricanes (approximately a hurricane every two years) pass within 75 nautical miles (Rappaport & Sheets, 1993). Further to the southeast, the island of San Salvador was directly struck by 13 hurricanes during 1899 to 1987, and during this same period another 20 hurricanes passed sufficiently close (160 km) to affect the island at a rate of a hurricane every 2.7 years (Shaklee, 1996).

HURRICANE PRODUCTION AND MAINTENANCE OF KW HABITAT

The predominant broadleaf forest type of pre-settlement times was believed to be a mixed evergreen-deciduous woodland or coppice (Campbell, 1978; Byrne, 1980). Much of this pre-settlement broadleaf woodland was likely tall coppice (>5 m tall), a habitat that does not appear to be used extensively by KWs (Lee *et al.*, 1997). However, the tall stature coppice woodlands are especially vulnerable to structural damage from hurricanes because trees with tall stature and large diameter trunks are more likely to snap or be uprooted than are smaller trees (Walker, 1991; You & Petty, 1991). Large branches of tall trees are also more vulnerable to breakage than are small branches, and these falling branches and tree trunks cause mortality of small understory trees and shrubs (Brokaw and Walker, 1991; Wunderle *et al.*, 1992). The structural damage to canopy trees creates canopy gaps, some of which may be enlarged when damage causes tree mortality. An example of hurricane-induced tree mortality relevant to tall coppice woodland comes from the structurally similar dry forest on limestone soils of Yucatan, Mexico, where 11.2% of the trees died in 17 months after Hurricane Gilbert, compared to 2.6% mortality 5 years before the storm (Whigham *et al.*, 1991). Thus, we expect hurricanes to radically alter the canopy structure of tall coppice forest from a mostly closed canopy with occasional gaps to a structure of many gaps with occasional areas of intact continuous canopy (e.g., Brokaw & Grear, 1991).

Alteration of the closed canopy of tall coppice woodlands by hurricanes increases light penetration to the understory, stimulating growth (*e.g.*, Fernández & Fetcher, 1991). Although initial understory regeneration may be temporarily delayed (3-6 months) due to leaf damage from increased UV radiation (You & Petty 1991), the predominance of foliage cover would temporarily shift from the canopy to lower levels until canopy closure (Brokaw & Grear, 1991; Wunderle *et al.*, 1992). More importantly, increased light stimulates flowering and fruiting of understory plants, which were previously limited by light availability (e.g., Levey, 1988a, 1988b; Loiselle & Blake, 1991). However, fruit set of some species might initially be constrained for several years after a hurricane by resource limitation, predation, or loss of pollinators (Rathcke, 2000, 2004). The importance of increased light for fruiting of understory shrubs would be especially important for shrubs with fruits consumed by KWs, such as wild coffee (*Psychotria* spp.) and wild guava (*Tetrazygia bicolor*), which appear to produce more fruit in light gaps than in shaded understory of tall coppice (Wunderle, Currie, and Ewert, pers. obs.). In addition to fruiting by understory shrubs, there may be fruiting by shade-intolerant pioneer species dispersed into the larger forest openings (Frangi & Lugo, 1991; Walker, 1991). Finally, an increase in arthropods is expected to occur with the flush of new leaves associated with recovery (Torres, 1992) and in response to the increase of storm debris (i.e., dead leaves) on the forest floor. The time period over which a regenerating forest opening might be attractive to a KW is unknown, given that the rate of canopy closure is a function of the extent of structural damage and other factors, including storm strength, species composition, edaphic conditions, and topography (reviewed in Brokaw & Walker, 1991).

The accumulation of storm debris would increase fire vulnerability of pine and even tall coppice in which natural fires are rare (Campbell, 1978). Pine forests are likely to be at greater risk to fires after hurricanes given the higher vulnerability of pines to structural damage (i.e., trunk snaps, uprooting) and mortality than hardwoods (Boucher *et al.*, 1990; Wunderle *et al.*, 1992). However, fires in hardwood or broadleaf forests in the wake of hurricanes are not unusual, and in some instances may be of natural origin, at least in Yucatan and Belize (Furley & Newey, 1979; Whigham *et al.*, 1991). Post-hurricane fires may be more important in altering forest structure than direct hurricane damage, especially on shallow and highly organic soils (Whigham *et al.*, 1990; Whigham & Cabrera Cano, 1991), which are characteristic of the blackland soils of The Bahamas (Sealey, 1994). Signs of post-hurricane fires were evident from our own casual inspections in April 2003 and 2005 of tall coppice sites damaged by Hurricane Andrew (in August 1992) in southern Eleuthera. Although it is likely that many of these post-hurricane fires were of human origin, some of the sites had flowering or fruiting individuals of plant species from which KWs are known to consume fruit (e.g., sage, black torch). Thus, post-hurricane fires are expected to accentuate both the degree and extent of a storm's damage, opening up previously mature sites to regeneration and colonization by early successional species.

Hurricane storm surges combined with wind-driven waves have the potential to physically remove island vegetation as well as to cause flooding of low lying areas, resulting in terrestrial plant mortality due to salt water inundation (e.g., Spiller *et al.*, 1998). The extent of plant mortality attributable to marine flooding associated with a strong hurricane could be considerable given the low elevation of islands in the archipelago. An example of the possible extent of vegetation loss was evident on North Eleuthera, where Hurricane Andrew's storm surge, combined with wave action, reached 7 m and pushed seawater inland for 1.5 km (Sealey, 1994). Although Hurricane Andrew was an especially powerful storm (category 4 on the Saphir-Simpson Scale), weaker storms can potentially generate destructive surges (e.g., category 3 hurricanes produce a surge of 2.5–3.7 m; Sealey 1994). Thus, Sealey (1994) estimates that any low lying coastal area within 4 m of sea level is at particularly high risk to storm surges. Although we are unaware of any studies of plant succession following vegetative loss due to saltwater inundation by storm surges, we suspect that this could be an important means of turning back plant succession. Early successional plant species would be expected to re-colonize the bare ground of these temporarily flooded sites once the salt was leached from the soils, which might occur relatively quickly after a storm in the coastal coppice zones characterized by sandy, porous soils.

In general, the early successional broadleaf or low coppice habitats favored by wintering KWs are not expected to sustain the degree of structural damage from hurricanes as expected in tall coppice woodlands, due to the smaller stem sizes typical of early seral stages (Walker, 1991; You & Petty, 1991; Wunderle *et al.*, 1992). In addition, the very high density of small flexible stems of many KW sites may be resistant to damage, although high stem density was associated with limited hurricane damage in two of three forest plots in the Virgin Islands (Reilly, 1991). However, the presence of wind-thrown shallow-rooted *Lantana involucrata* and *L. bahamensis* on shallow soils at a 5–7 year-old KW site on Eleuthera (Wunderle, Currie, and Ewert, unpubl. obs.) suggests that hurricanes may also set back succession in the earliest seral stages. Moreover, storm damage to the tallest trees and shrubs on early seral sites may delay maturation of the site and prolong the time period over which the site is suitable for use by wintering KWs. Therefore, not only is it likely that hurricanes can produce new KW habitat by opening up closed canopy of tall coppice, but hurricanes may prolong the "life" of existing KW sites, by setting back or delaying succession.

SUMMARY

Previous observations and our own findings indicate that KWs routinely use early successional shrubby habitats in The Bahamas. Our research findings to date indicate that wintering KWs readily shift locations on Eleuthera as they track food abundance (especially fruit) as it waxes and wanes at different sites over the course of a winter. The use of early successional stages and pattern of winter movements that allows opportunistic use of the richest available food patches is consistent with a disturbance-adapted foraging strategy. As a disturbance-adapted species on the wintering ground, KWs are expected to use early successional habitats resulting from either anthropogenic or natural disturbance. In pre-settlement times, recurring fires may have been an important source of natural disturbance on the pine islands, which were probably augmented by hurricanes and which likely played a dominant role as a disturbance factor on the coppice-covered islands without pines. By reducing or even eliminating canopy (i.e., blow-down sites) of tall coppice, hurricanes stimulate understory growth, which favors regeneration of fruiting shrubs. In addition, hurricane storm surges in low-lying coastal areas are also expected to create early-successional patches, some of which may be used by KWs. As a result of anthropogenic disturbance, some of our KW winter sites could have the physiognomy, species composition, and fruiting plants associated with hurricane-damaged sites. However, no studies of KWs have yet been conducted in sites seriously damaged by hurricanes. Therefore, this hypothesis remains to be tested, especially because of its conservation importance for understanding how KW winter habitats are produced.

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