The Impact of Variation in Stopover Habitat Quality on Migrant Rufous Hummingbirds

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Abstract: *We examined the impact of variation in habitat quality on migrating Rufous Hummingbirds* (Selasphorus rufus) *in the California Sierra Nevada. As do other migratory species, these birds depend on "stopover" habitats en route for feeding and replenishing depleted energy stores. During seven years of study, the quality of the stopover habitat (assessed in terms of the density of nectar food resources) varied widely due to natural variation in flowering. In years when stopover habitat quality was poor, incoming body masses were low and stopover durations were long. Population densities of migrant hummingbirds at the study site were coupled to habitat quality both within and among years. These observations demonstrate important effects of stopover habitat variation on the physiological, behavioral, and population ecology of migrating hummingbirds. High-quality stopover habitats are critical links between breeding and wintering areas for many species, and their preservation should be considered an essential component of strategies aiming to conserve migratory bird populations.*

Impacto de la variación en la calidad de los hábitats de las paradas intermedias en Colibríes ("Rufous Hummingbirds") migratorios

Resumen: *Examinamos el impacto en la variación de la calidad del hábitat en Colibríes migratorios* (Selasphorus rufus) *en la Sierra Nevada de California. Estos pájaros, al igual que otras especies migratorias dependen de "stopover" (paradas intermedias) en su ruta para alimentarse y reestablecer el almacenamiento de energía perdida. Durante los siete años de estudio, la calidad de los hábitats de las paradas intermedias (evaluada en términos de la densidad de néctar de los recursos alimenticios) varió ampliamente debido a la variación natural de la floración. En los años en los que la calidad del hábitat de las paradas intermedias fue pobre, la masa corporal de llegada fue baja y la duración de la estadía en la parada fue más larga. Las densidades de población de los Colibríes migratorios en el sitio de estudio estuvieron relacionadas con la calidad del hábitat dentro y entre años. Estas observaciones demuestran impactos importantes en la variación fisiológica, en el comportamiento y en la ecológica de poblaciones de los Colibríes migratorios. La alta calidad del hábitat de las paradas intermedias es crítica en el lazo entre áreas de cría y de invernada para muchas especies y su preservación debería ser considerada un componente esencial de las estrategias dirigidas a conservar las poblaciones de aves migratorias.*

Introduction

Recent studies have documented population declines in a variety of migratory landbird species that breed in northern areas and winter in the Neotropics (reviewed by Askins et al. 1990; Finch 1991; Morton 1992), but reasons for these declines remain controversial (see Hutto 1988; Terborgh 1989). Explanations proposed to date have focused on habitat alteration occurring in northern breeding areas (e.g., Wilcove 1985; Askins & Philbrick 1987; Askins et al. 1987; Leck et al. 1988) and/or in tropical wintering areas (e.g., Ambuel & Temple 1982; Hall 1984; Marshall 1988; Robins et al. 1989). In contrast, relatively few workers have explicitly considered the possibility that habitat alteration occurring *between* the breeding and wintering grounds might contribute significantly to population trends (see Finch 1991; Moore & Simons 1992). The comparative lack of attention paid to this possibility is surprising, in light of the demonstrably large impact of events en route on many migratory bird populations (e.g., Ketterson & Nolan 1982; Lindström 1989; Owen & Black 1991).

Because many species of migrants are not physiologically capable of storing enough fuel to power the entire migratory flight, they must stop frequently while en route and replenish their energy stores. Habitat use during these stopovers affects a migrant's feeding efficiency, its vulnerability to predation, and its exposure to environmental stresses (Graber & Graber 1983; Lindström 1990; Moore et al. 1990; Moore & Yong 1991; Moore & Simons 1992). Changes in the availability of suitable stopover habitats could therefore have important effects on a migrant's ability to successfully complete a migration, and Moore and Simons (1992:353) recently argued that "factors associated with the en route ecology of migrants must figure in any analysis of population change and in the development of a comprehensive conservation 'strategy' for Neotropical wintering landbird migrants."

In this paper we focus on the relationship between en route habitat quality and the ability of migrants to meet their energy requirements. We studied southbound migrant Rufous Hummingbirds (*Selasphorus rufus*) at a California stopover site for seven consecutive years (1980–1986). During this seven-year period, we observed substantial natural variability in the density of the flowers that produce the nectar on which the hummingbirds feed. Here we present data on the ecological consequences of this natural variation. Our premise is that understanding how natural variability in stopover habitats affects migrants can serve as a useful starting point for addressing the conservation implications of human-caused loss or degradation of stopover habitats.

Natural History and Methods

Rufous Hummingbirds breed in the Pacific Northwest and migrate during the summer along the Cascade–Sierra Nevada and Rocky Mountain ranges to their wintering grounds in Mexico (Grant & Grant 1967; Phillips 1975; Calder 1987). The birds require several refueling stopovers while en route. These stopovers take place in mountain meadows, where birds establish temporary territories around patches of flowers (Gass 1979; Hixon et al. 1983). Competition for exclusive access to these flower patches is usually intense (Kodric-Brown & Brown 1978; Hixon et al. 1983), and not all birds are able to acquire territories (Carpenter et al. 1993*b*).

Once a migrant has acquired a territory and begun to refuel, several days to three weeks are required to reach a final mass of about 4.6 grams, whereupon the migratory journey is usually resumed (Carpenter et al. 1983, 1993*a*). Mass changes in migrant hummingbirds are accompanied by changes in body composition that can have important effects on a bird's ability to refuel rapidly and efficiently (Carpenter et al. 1993*a*). At body masses above 3.5 grams, most mass variation is due to the deposition and catabolism of fat, which is the primary energy source for migration. In contrast, mass changes below a body mass of 3.5 grams are due to variation in fat-free dry mass and water, probably associated with flight muscle repair in birds that deplete their fat stores and resort to muscle as an emergency energy source. Birds whose body masses fall below 3.5 grams may have a survival disadvantage, because redeposition of the nonfat mass is apparently a slower and more costly process than is fat deposition (Carpenter et al. 1993*a*).

Our study site was a 2-ha stream-fed meadow in sagebrush scrub desert at the base of the eastern Sierra Nevada, 27 km northwest of the town of Bishop, California (37° 30' N, 118° 30' W, 1700 meters elevation). A grassy zone associated with the stream supports the hummingbird-visited plant *Castilleja linariaefolia* (Scrophulariaceae). The habitat is open, allowing continuous observation of bird behavior from 6-foot ladders placed outside territories.

The data reported here were collected at this site each summer from 1980 to 1986. Southbound Rufous Hummingbirds usually arrived between late July and early August, and the 2 ha of *Castilleja* supported up to 50 exclusive territories at any given time (Carpenter 1987). We captured birds with mist-nets, weighed them, and color-marked them with narrow strips of colored surveyor's flagging glued to the skin of the back. These strips did not add detectably to their mass and did not seem to bother the birds. Because many of the birds captured and weighed during the first day of netting each year had already been resident in the meadow for

an unknown amount of time, data on these individuals are not included in this paper.

Each day, we mapped the locations of all marked and unmarked territory owners in the meadow. Our netting, marking, and mapping allowed us to estimate stopover durations for large numbers of territorial birds. Although we often observed birds initiating migratory departures, it was not possible to know precisely when each bird arrived. We estimated the stopover duration for an individual bird as the number of full days between our initial detection of the bird in the meadow (either through netting, or by visual observation of a new territory owner who was subsequently captured and marked) and its departure from the meadow. For example, the estimated stopover duration of a bird initially captured during the evening on August 1 and observed departing on the morning of August 10 would be eight days.

In order to assess interannual differences in migration traffic (numbers of hummingbirds passing through the study site), we calculated two indices for each of the seven years of our study. The first index is a measure of average migration traffic rate, calculated as the cumulative number of hummingbirds netted over the course of a season divided by total netting effort in net-hours. The second index is a measure of the peak migration traffic rate, and is calculated as the number of hummingbirds netted per unit netting effort on the peak flight day. Days with low sampling effort (≤ 30 net-hours) were excluded from the determination of peak flight days to avoid statistical artifacts generated by small samples.

Each summer at the time of peak flowering, we counted flowers along two permanent, 2-meter-wide transects through the *Castilleja*, one 36 meters long and one 50 meters long. Mean flower density in the meadow was estimated by dividing the total number of flowers counted by the total area in which counts were made. In this paper, we use the peak mean flower density in the meadow as a measure of the quality of the stopover habitat for each year.

Results

Effects of Stopover Habitat Quality on Individual Migrants

During the seven years of study, we captured and weighed exactly 1800 rufous hummingbirds. The frequency distribution of body masses of migrants upon their initial capture in the meadow is nearly normal in the upper range, but is extremely nonnormal in the lower range (Fig. 1). Specifically, sharp drop-offs in numbers of migrants captured are evident below 3.2 grams and especially below 3.0 grams. As described earlier, mass changes in birds weighing less than 3.5 grams involved variation in nonfat dry mass that is thought to
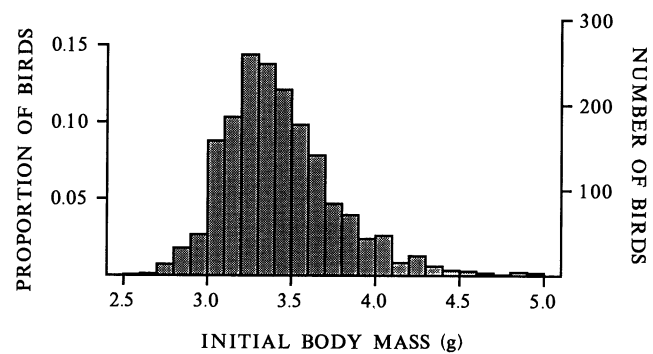

Figure 1. Frequency distribution of body masses of exactly 1800 migrant hummingbirds upon initial capture in the meadow.

represent metabolism of muscle tissue in fat-depleted migrants. Because of this pattern, we suspect that the disproportionately low numbers of migrants with body masses below 3.0 grams reflect high mortality among such individuals. (A fuller justification of this assumption is provided in the Discussion.) We therefore classified birds as having either "low" (≤ 3.0 grams) or "high" (>3.0 grams) body masses upon initial capture.

Relative numbers of birds with low and high body masses upon initial capture varied significantly among the seven years of study ($X^2 = 106.9$, $n = 1800$, df = 6, $p \ll 10^{-9}$). The percentage of birds with low body masses showed a strong inverse relationship with peak flower density in the meadow (Fig. 2a; *percent* = $44.2 - 2.2*density$, $n = 7$, $r^2 = 0.94$, $p < 0.001$).

Stopover durations of birds that established territories in the meadow varied greatly within and among years, but variances were homogeneous among the seven years of study (Bartlett's test, $X^2 = 6.8$, df = 6, $p = 0.34$). Among years, average stopover duration was inversely related to peak flower density (Fig. 2b). This relationship did not vary among the four age-sex classes (adult males, immature males, adult females, and immature females; ANCOVA: $F_{3,218} = 0.19$, $p = 0.90$). The overall regression equation was *stopover* = $11.76 - 0.43*density$, $n = 226$, $r^2 = 0.15$, $p < 10^{-8}$).

Effects of Stopover Habitat Quality on Populations of Migrants

Peak migration traffic rate of hummingbirds and peak flowering in the meadow both varied by about a month among the years of study, but these peaks were positively correlated across years (Fig. 3; *migration* = $51.2 + 0.8*flowering$, $n = 7$, $r^2 = 0.72$, $p = 0.016$).

Migration traffic rates estimated on peak flight days and averaged over the season showed similar interannual trends (Fig. 4). Interannual declines in both measures were evident between 1980 and 1981 and be-
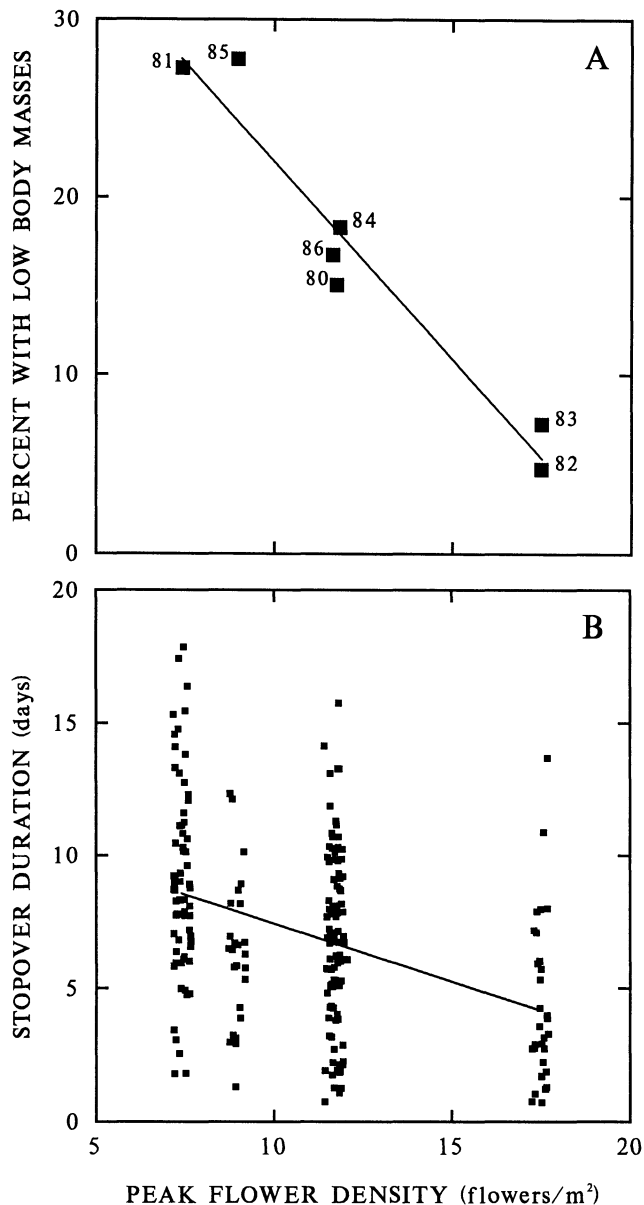
Figure 2. (a) Proportion of birds with "low" ($\leq$ 3.0 grams) body mass upon initial capture at the study site in relation to peak flower density in the habitat. (b) Stopover durations of 226 migrants that established territories in relation to peak flower density in each year of the study. For illustrative purposes, a small amount of uniform random error has been added to all data points to avoid overlap.

tween 1984 and 1985, and a rapid increase in both measures was evident between 1982 and 1984.

Discussion

En Route Ecology of Migrating Hummingbirds

Our data show that more migrant hummingbirds had low body masses upon initial capture at our study site in years when the quality of the habitat was poor than in years when habitat quality was high. Variation in initial capture masses could reflect either variation in body masses of newly arrived migrants or variation in feeding conditions experienced by these migrants following their arrival. The latter explanation seems highly unlikely because as we have shown elsewhere (Carpenter

et al. 1993a), rates of body mass change are very low in migrants weighing less than 3.5 grams, and these rates seem to be physiologically constrained rather than subject to environmental influences. Therefore, we believe that the pattern documented in Fig. 2a reflects interannual differences in the body masses at which birds arrived at our study site.

If interannual differences in initial body masses of migrant hummingbirds do reflect offsite influences, then the strong correlation between initial mass and onsite conditions suggests that flower densities at our study site were correlated with flower densities encountered by birds at other stopover sites along their migration route. Is spatial coherence in regional flowering intensity biologically plausible? Although we lack quantita-
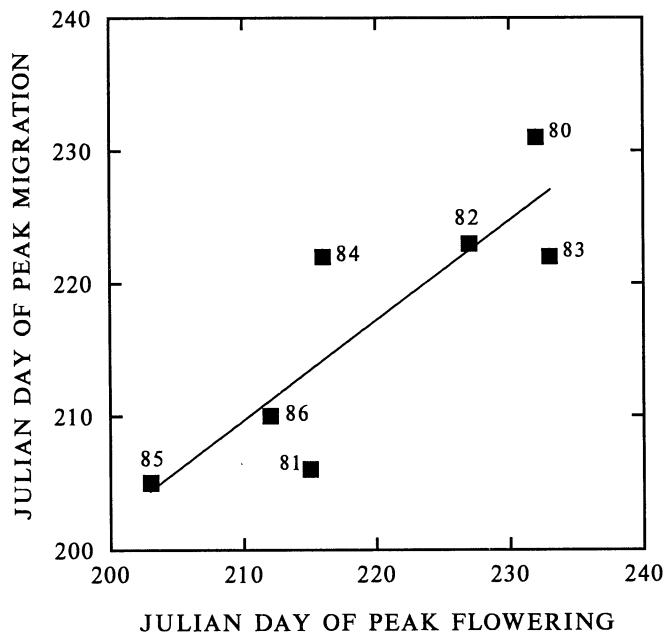
Figure 3. Interannual variation in the seasonal timing of peak migration traffic rate in relation to peak flowering at the study site. Julian day 200 is July 19, and Julian day 240 is August 28.

ing water resources in the form of rain, or more indirectly by increasing the snowpack. Snowpack along the Cascades–Sierra Nevada migration route may affect stopover habitats either by providing insulation to over-wintering plants or via the availability of snowmelt run-off to plants during dry periods. In studies of another hummingbird-visited plant, *Delphinium nelsonii*, Inouye and McGuire (1991) showed that flowering was delayed and peak floral abundance was reduced in years of low snow accumulation in the Colorado Rocky Mountains.

Did variation in stopover habitat quality have important consequences for hummingbird survival? Three lines of evidence from our study suggest that it did. First, our data show that birds spent more time at our stopover site in flower-poor years (Fig. 2*b*), indicating that the progress of migration was delayed. The ability to proceed southward rapidly is particularly important to migrating hummingbirds, because the suitability of their stopover habitat is temporally bounded by flowering periods. Furthermore, slow-moving migrants face deteriorating weather in late summer along their migration route, and they may then be caught in storms and prevented from feeding (Gass & Lertzman 1980; Carpenter & Hixon 1988).

Second, the truncated statistical distribution of the body masses of migrants (Fig. 1) suggests selection against birds whose masses fall below 3.0 grams, and

tive data from other stopover sites, anecdotal evidence is consistent with this explanation. In 1982, we conducted several days of observations at other meadows up to 40 km to the north that we had studied in previous years (1976–1980). Flower densities at these sites were obviously much higher than in the previous years, as was the case at our principal study site (Fig. 2).

Synchronous variation in weather patterns over a broad area represents one possible source of coherence in the timing and intensity of flowering at regional spatial scales. It is interesting to note that 1981 and 1985, the two years when habitat quality was poorest (Fig. 2), were unusually dry summers over large areas of the western United States (Dickson 1981; Livezey 1981; Taubensee 1981; Wagner 1981; Bergman & O'Lenic 1986). At our study site, *Castilleja* flowers seemed to be in generally poor condition in these years, and they desiccated quickly. At the opposite extreme, one of the most intense El Niño–Southern Oscillations (ENSOs) on record occurred in 1982 and 1983 (Quinn et al. 1987), the years when habitat quality was highest at our study site (Fig. 2). Ropelewski and Halpert (1986, 1987) showed that precipitation levels were consistently above normal throughout the Great Basin region during this ENSO episode. Anomalously high precipitation over much of the Rufous Hummingbird's migration corridor may have enhanced the availability and quality of stopover habitat on a regional basis. High precipitation could affect stopover habitat either directly, by provid-
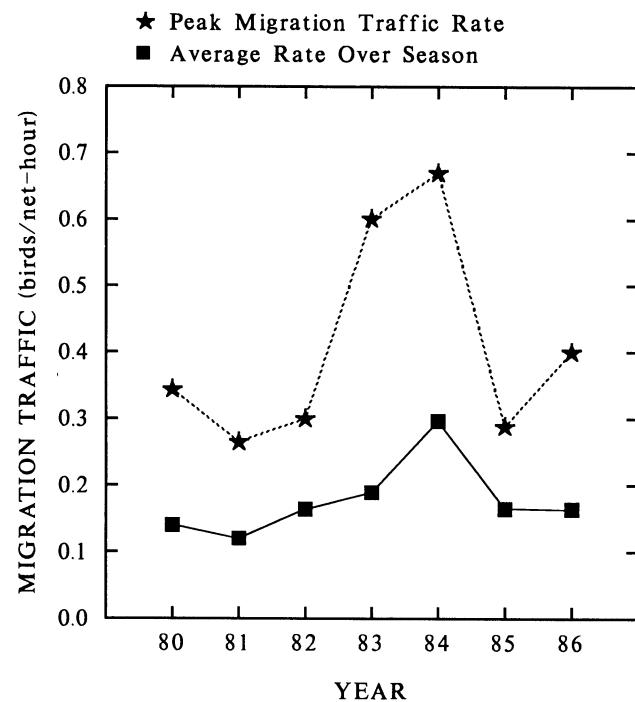

Figure 4. Interannual trends in migration traffic rates measured on the peak flight day (top) and averaged over the season (bottom) in each year of study.

perhaps even below 3.2 grams. In most years, food was limited at our stopover site (in other words, the availability of flower nectar was low relative to the numbers of birds), and all flower patches were vigorously defended. Under these circumstances, incoming migrants with low body masses have few options. One option is to wait until a defended territory is vacated by a departing migrant. Because of their extremely high metabolisms (Pearson 1950; Lasiewski 1963; Epting 1980), however, hummingbirds cannot afford to wait for very long without access to food. Another option is to "poach" nectar from another bird's territory (Paton & Carpenter 1984; Carpenter et al. 1991, 1993c). The boldest option is to attempt to displace another bird from its territory. Successful displacement of territorial birds by individuals without territories is uncommon, however; during 7 years of study, we only observed 12 cases (Carpenter et al. 1993b). A minority of the birds captured at our study site eventually acquired territories, and most undoubtedly proceeded southward in search of suitable, unoccupied stopover habitat elsewhere. But birds that continue the migratory journey without having successfully refueled probably face a very uncertain future. Low fuel stores severely limit the area in which migrants can search, and because of the patchy distribution of flowering meadows along the migration route, discovery of suitable habitat before body reserves are completely exhausted is far from guaranteed. We have no data on the ultimate fate of such birds, but numerous anecdotal observations (e.g., Miller 1963; Kodric-Brown & Brown 1978) suggest that starvation of migrant Rufous Hummingbirds while en route is not uncommon.

Third, the data shown in Fig. 4 provide suggestive evidence of major population-level consequences. Declines in hummingbird migration traffic were evident in the two years when stopover habitat quality was poorest, 1981 and 1985. More intriguingly, increases in migration traffic occurred not only through the two years of highest flower densities (1982–1983), but also into the following year (1984), when stopover habitat quality was average relative to other years of our study (see Fig. 2a). This observation is consistent with a lagged numerical response, suggesting that interannual variations in migration traffic at our study site reflected overall population dynamics and not simply an aggregative response of migrants to locally high resource densities (see Martin & Karr 1986).

Conservation Implications

The montane meadows used by migrating Rufous Hummingbirds are not immediately threatened. However, stopover habitats for many other species are currently subject to increasing rates of degradation via real estate development along other important migration flyways (for example, along the middle Atlantic coast [McCann

et al. 1993] and along the northern coast of the Gulf of Mexico [Moore & Simons 1992]). Remnant habitats may become so fragmented and/or degraded as to be nearly unusable by migrants. Loss of stopover habitat could reduce the birds' chances of completing a migration successfully either by directly precluding the possibility of feeding or by intensifying competition among migrants for increasingly limited food resources. If our results on Rufous Hummingbirds can be generalized to other species of long-distance migrants, then habitat degradation along migration routes might indeed be implicated in some of the population declines recently reported, and it should certainly be considered in future analyses of population change.

The development of effective prioritization schemes (e.g., Hunter et al. 1993) to guide conservation programs targeting the en route habitats of migratory landbirds will face particularly formidable challenges. Although recent efforts to conserve stopover habitats of transhemispheric migratory shorebirds have been notably successful (Myers et al. 1987; Payne 1991), there are important differences between shorebird and landbird migrations. Because many shorebird species pass through "geographic bottlenecks" where large proportions of the population are concentrated in restricted areas (Myers 1983), preservation of a relatively small number of critical sites along the migratory route can be a powerful yet economically and logistically feasible conservation strategy (Myers et al. 1987).

In contrast, most species of migratory landbirds do not have such clearly defined migration pathways, and individual migrants are likely to be much more widely dispersed throughout appropriate habitats between wintering and breeding areas. In this case, just the identification of important sites for preservation and/or management poses substantial practical difficulties, because so little is known about the en route habitat requirements of migrant landbirds. To what extent are migrant landbirds behaviorally flexible in their selection of stopover habitat while en route? Which habitats are exploited by the largest numbers of migrants? Can very small habitat patches support the high energy requirements of migrants? Such questions must be addressed for a variety of species before challenges facing migratory landbird conservation can be addressed effectively.

Acknowledgments

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