A COMPUTER PROGRAM FOR GUILDING SPECIES' RESPONSES TO HABITAT CHANGES BASED ON THE CALIFORNIA WILDLIFE HABITAT RELATIONSHIPS SYSTEM

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Abstract: The California Wildlife Habitat Relationships (CWHR) system includes a habitat classification system and habitat suitability models for the approximately 650 species of terrestrial vertebrates that use these habitats. We created a computer model for grouping these species into guilds based on how the habitat suitability of forest-dwelling wildlife is predicted by CWHR to respond to changes in average tree diameter and percent forest canopy cover. We found that the largest bird guilds in Sierran mixed conifer habitat were: (1) species for which reproductive and cover habitat quality improved as average tree size increased; (2) species for which foraging habitat quality worsened as forest canopy cover increased; and (3) generalist species that showed no substantial change in habitat quality with respect to a particular life function as average tree size or forest canopy cover increased. We found that the predicted responses by the guilds from the model were generally consistent with several published lists enumerating species' sensitivities to habitat changes comparable to that modeled for the guilds. In conclusion, we suggest that our model may provide a useful tool for elucidating general biodiversity patterns in cumulative impacts and landscape resource assessments.

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Key words: California, computer model, cumulative impact assessment, forest habitats, landscape resource assessment, wildlife guilds, wildlife habitat relationships.

Root (1967) was among the first to use the guild concept for grouping species of wildlife, which he defined as "a group of species that exploit the same class of environmental resources in a similar way" (1967:335). Root (1967) also identified several uses for the concept including (1) identifying those species that are competing for similar resources within a given area, and (2) facilitating the comparative study of communities by considering the ecological requirements of animals across taxonomic groups. Examples of guilds described by various researchers include the cavity-nesting bird guild composed of the hairy woodpecker (*Picoides villosus*), brown-headed nuthatch (*Sitta pusilla*), eastern screech owl (*Otus asio*), and other species (Canterbury et al. 2000), and the insectivorous ground-gleaning foraging bird guild composed of the killdeer (*Charadrius vociferus*), cattle egret (*Bubulcus ibis*), mountain bluebird (*Sialia currucoides*), and other species (DeGraaf et al. 1985).

The application of the guild idea to environmental impact assessment has been controversial because it is linked to using indicator species within a guild to measure responses to management actions (Simberloff and Dayan 1991). The clear benefit of using guilds in environmental impact assessment is that an understanding of the habitat requirements of guilds of animals reduces the complexity faced by biologists when assessing the effects of individual habitat changes to the hundreds of species that may use a given area. Severinghaus (1981:187) reasoned that "once the impact on any one species in a guild is determined, the impact on every other species in the guild is known." This logic led to the use of indicator species, such as the spotted owl (*Strix occidentalis*), for assessing and monitoring impacts on multiple animals within a guild. The

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use of guilds and indicator species in impact assessment, however, has been criticized by some as overly simplistic and inappropriately applied (Simberloff and Dayan 1991, Mannan et al. 1983). Others have acknowledged these problems, but they also suggested that careful and qualified use of guilds and indicators still plays a role in impact assessment (Landres 1983, Laudenslayer 1991).

The California Wildlife Habitat Relationships (CWHR) system rates the habitat quality for the reproductive, cover, and foraging requirements of >650 terrestrial wildlife species in the various size and density stages of numerous forest, shrub, and herbaceous communities found throughout California (Airola 1988). For example, the CWHR models rate the quality of reproductive habitat for northern goshawk (*Accipiter gentilis*) in dense, mature Sierran mixed conifer habitat as high, and the quality of foraging habitat in all stages of mixed chaparral habitat as low. Goodfellow and Mayer (1983) explored methods for placing species in guilds based on the habitat preference patterns predicted by CWHR. They used multivariate cluster analysis and a simple sorting procedure to identify groups of species with preferences for similar size and stages of canopy closure of particular habitat types.

In this paper, we describe a new attempt at grouping wildlife species into guilds that corresponds to similar habitat preferences of the species within the guilds. The California Department of Fish and Game (DFG) participates in the review of timber harvesting plans on private lands in California. To better assess cumulative timber harvesting impacts, there is a need to quantify the tradeoffs between detrimental and beneficial impacts on wildlife occurring in watersheds with historical and proposed future timber harvesting. On one hand, logging may reduce the availability of large trees used by some wildlife, while at the same time, some types of silviculture may help restore early seral habitats in fire-suppressed forests where these habitats are rare. To help in the evaluation of cumulative impacts, we collaborated to develop software for guilding species based on information contained in the CWHR models. The new software described here applies an approach to assigning guilds similar to that used by Goodfellow and Mayer (1983). The current work, however, analyzes CWHR species models in terms of their sensitivity to changes in forest structural conditions (e.g., increasing canopy cover), whereas the previous work focused on absolute preferences of animals for specific habitat stages (e.g., a particular combination of CWHR forest habitat type, and tree size and canopy closure classes). The primary purpose for developing the guild software described in this paper was to aid assessment of cumulative impacts and landscape resource. We did not intend to make assessments using a single indicator species within a particular guild, as cautioned against by Simberloff and Dayan (1991). Conversely, our intent was to broaden the scope of impact assessment beyond a few threatened or endangered species to encompass guilds of wildlife species associated with different sets of habitat conditions at the landscape scale.

METHODS

California Wildlife Habitat Relationships

The CWHR system classifies 23 different types of forest and woodland habitats (Mayer and Laudenslayer 1988) (Table 1). Each habitat type includes categories for tree size and canopy cover (Table 2). Size is measured as the quadratic mean diameter of all sampled trees $\geq$13 cm diameter at breast height within the habitat. Canopy cover is the average % canopy cover for the overstory trees.

The CWHR models have habitat quality ratings for each of approximately 650 terrestrial vertebrate species known to occur in California. These ratings apply to all possible combinations of size and canopy cover classes in every CWHR habitat type in which a species is predicted to occur. To distinguish between habitat quality for different life functions, reproductive, cover, and foraging habitats are rated separately. The definitions for CWHR habitat quality ratings (Airola 1988:19) are as follows: High (H)—habitat is optimal for species occurrence and it can support relatively high population densities at high frequencies; Moderate (M)—habitat is suitable for species occurrence and it can support relatively moderate population densities at moderate frequencies; Low (L)—habitat is marginal for species occurrence and it can support relatively low population densities at low frequencies; Unsuitable (U)—habitat is unsuitable for species occurrence and the species is not expected to occur in the habitat. A complete description of CWHR habitat classifications and modeling is provided by Mayer and Laudenslayer (1988), Airola (1988), and the DFG (http://www.dfg.ca.gov/whdab/html/cwhr.html).

Table 1. Forest and woodland habitat types included in the California Wildlife Habitat Relationships system.

Habitat types
Aspen
Blue oak-foothill pine
Blue oak woodland
Coastal oak woodland
Closed-cone pine-cypress
Douglas-fir
Eastside pine
Jeffrey pine
Juniper
Klamath mixed conifer
Lodgepole pine
Montane hardwood-conifer
Montane hardwood
Montane riparian
Pinyon-juniper
Ponderosa pine
Redwood
Red fir
Subalpine conifer
Sierran mixed conifer
Valley oak woodland
Valley foothill riparian
White fir

Guild Software

We developed a wildlife guild assignment computer program called Habitat Utilization Guilds Software (HUGS), which is a stand-alone application written in the Pascal programming language (Fig. 1). The model applies to forest and woodland habitats throughout California that cover approximately 12.5 million ha (California Department of Forestry and Fire Protection 2002). Wildlife species are assigned by HUGS to response guilds based on how habitat suitability is affected by changes in forest tree size and canopy closure, as modeled in CWHR. The HUGS program was beta tested by a group of state, federal, and timber company scientists in 2003. The computer program is available for use and can be downloaded from the DFG at http://ncncr-isb.dfg.ca.gov/itp/, or ordered by sending a request to the senior author. Some of the comments received from the beta-testing review were incorporated into the initial version of HUGS.

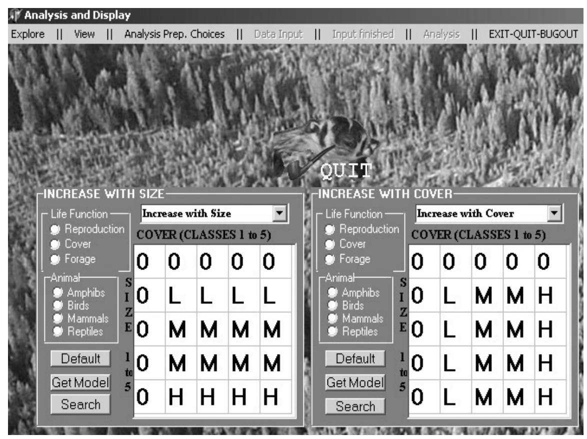

Fig. 1. Partial screen view of the Habitat Utilization Guilds Software user interface.

Recommendations requiring more extensive changes may be incorporated into later versions of the program. Currently, the downloadable HUGS package includes the software described here, supplemental Microsoft ® Excel[2] macro applications for creating lists and graphs summarizing HUGS and standard CWHR outputs, and a user manual for the software (Furnas 2004).

Wildlife species' responses to habitat suitability were evaluated by HUGS as tree size

[2] The use of this product does not indicate endorsement by the California Department of Fish and Game.

Table 2. Definitions of size and canopy classes for forested habitats in the California Wildlife Habitat Relationships system.

Size class	QMD[a] (cm)	Canopy closure class	Cover (%)
1	<3	S	10–25
2	3–15	P	25–40
3	15–28	M	40–60
4	28–61	D	60–100
5	>61		

[a] QMD is quadratic mean diameter at breast height (1.4 m) of trees sampled in the forest stand.

and canopy cover increased in forest and woodland habitats. The first step in the process was to transform the CWHR model into a 2-dimensional matrix where size and canopy were independent dimensions (Fig. 2). An example of the pattern expressed in the matrix (Fig. 2) for mountain bluebird in eastside pine habitat indicated a strong relationship between decreasing habitat quality and increasing canopy cover (i.e., "Down With Cover"), and a moderate relationship between increasing habitat quality and increasing average tree diameter size (i.e., "Up With Size"). Taken as a single pattern, the model could be described as "Up Size Down Cover."

A series of algorithms was used by HUGS to quantitatively assign guilds based on species–habitat combinations. The CWHR model pattern for a given species–habitat combination was converted into a numerical matrix using the following default parameters: high (H) = 8, moderate (M) = 6, low (L) = 4, and unsuitable (U) = 3. Next, the 4 by 4 portion of the matrix representing size classes 2, 3, 4, and 5 and canopy classes S, P, M, and D was split into 2 by 4 blocks representing either high cover (D, M) and low cover (P, S), or large size (5, 4) and small size (3, 2) (Fig. 3). It is important to note that non-suitable ratings were given a non-zero value of 3.

Canopy Cover Class (increasing -->)

Size Class (<-- increasing)	S	P	M	D
2	L	L	U	U
3	M	M	U	U
4	H	M	U	U
5	H	M	U	U

↓

Canopy Cover Class (increasing -->)

Size Class (<-- increasing)	S	P	M	D
2	4	4	3	3
3	6	6	3	3
4	8	6	3	3
5	8	6	3	3

Fig. 2. An example of matrix transformation of the California Wildlife Habitat Relationships system reproductive habitat suitability model for mountain bluebird in eastside pine habitat.

Average values of the cells in each block and the ratio of the block values were calculated (Fig. 3). If the average value for the second block was greater than the average value for the first block, the pattern was "Up With Size" or "Up With Cover." On the other hand, if the second block value was less than the first block value, the pattern was "Down With Size" or "Down With Cover." The ratio of the 2 average block values was used to determine the strength of the pattern based on the following parameters: >1.7 for high strength and 1.2–1.7 for medium strength. If the strength ratio <1.2, the guild pattern was labeled as "No Pattern." It is

Cover Pattern Test

size\cover	S	P	M	D
2	4	4	3	3
3	6	6	3	3
4	8	6	3	3
5	8	6	3	3
	Avg = 6		Avg = 3	

Block Ratio = 2.00, high strength 1-dimensional guild = down with cover.

Size Pattern Test

size\cover	S	P	M	D	
2	4	4	3	3	Avg = 4
3	6	6	3	3	
4	8	6	3	3	Avg = 5
5	8	6	3	3	

Block Ratio = 1.25, medium strength 1-dimensional guild = up with size.

Fig. 3. An example of the Habitat Utilization Guilds Software guild assignment algorithm for the reproductive habitat suitability model for mountain bluebird in eastside pine habitat.

important to note that the choice of suitability values and strength filter parameters was arbitrary. The default parameters used in HUGS were chosen because we felt these numbers yielded biologically meaningful results for guild assignment when we tried different values during development of the software. However, HUGS allows users to change the settings in the guild assignment algorithms.

The primary algorithms assigned species in a particular habitat to both tree size and canopy cover response guilds. Each species belongs independently to size and cover guilds. However, a secondary set of algorithms compared the relative strengths of size and cover patterns and assigned each species–habitat combination to a single size and cover guild, such as "Up Size Down Cover" calculated for the mountain bluebird in eastside pine habitat. Size- and cover-independent guilds were 1-dimensional guilds, whereas the guilds assigned using the secondary comparative process were 2-dimensional guilds.

RESULTS

Many varieties of queries can be analyzed with HUGS. For example, all wildlife species predicted to occur in any of the 23 forest and woodland habitat types can be assigned to 1-dimensional or 2-dimensional guilds for each of the 3 life functions. Alternatively, guild analyses can be run on a list of user-selected species, such as a list of prey species for fisher (*Martes pennanti*).

For demonstration purposes, we ran HUGS to assign 1-dimensional guilds to the 99 bird species predicted by CWHR to occur within Sierran mixed conifer habitat at moderate or high suitability levels (Fig. 4). Membership in the no-pattern guilds was large across all life functions, with a peak of 73% for "No Size Pattern" with respect to forage. The red-tailed hawk (*Buteo jamaicensis*), dusky flycatcher (*Empidonax oberholseri*), and common nighthawk (*Chordeiles minor*) were examples of birds in this guild. The pattern guilds with the largest memberships were "Up with Size" for reproduction and cover, each containing 66% and 56%, respectively, of queried species. Northern flicker (*Colaptes auratus*), osprey (*Pandion haliaetus*), and red-breasted nuthatch (*Sitta canadensis*) were examples of birds in the "Up with Size" reproductive guild. The third largest pattern guild was "Down with Cover" for forage containing only 31% of species. American robin (*Turdus migratorius*), calliope hummingbird (*Stellula calliope*), and golden eagle (*Aquila chrysaetos*) were examples of birds in this guild.

We also ran HUGS to assign 2-dimensional guilds to bird species predicted in CWHR to occur within Sierran mixed conifer habitat at moderate or high suitability levels (Fig. 5). The 3 largest pattern guilds were still "Up with Size" for reproduction and cover, and "Down with Cover" for forage, but membership in these guilds dropped to 40% for the former 2 guilds

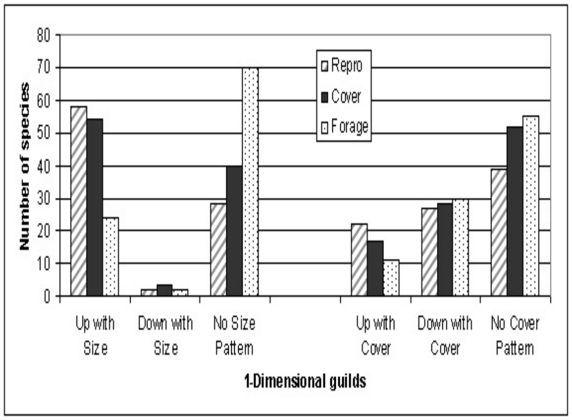

Fig. 4. One-dimensional Habitat Utilization Guilds Software guilds for birds predicted to occur in Sierran mixed conifer habitats at moderate and high suitability ratings from the California Wildlife Habitat Relationships system.

and remained constant at 30% for the latter guild. Similarly, membership in the no-pattern guilds dropped, although less so with respect to forage. The cause for these drops was that the secondary guild algorithm reassigned a number of species to combination pattern guilds. For example, 11% of birds were grouped in the “Up Size and Cover” reproductive guild, including spotted owl, northern goshawk, and pileated woodpecker (*Dryocopus pileatus*), whereas 10% were grouped in the “Up Size Down Cover” reproductive guild, including red-breasted sapsucker (*Sphyrapicus ruber*), purple martin (*Progne subis*), and western bluebird (*S. mexicana*).

Finally, we ran HUGS to assign 2-dimensional guilds to 8 common prey species of northern goshawk in Sierran mixed conifer habitat where the prey list was derived from the findings of Bloom et al. (1985) (Table 3). Seven species were in either the “Up with Size” or “Up Size and Cover” reproductive guilds. In contrast, only 4 species were assigned similarly with respect to foraging, whereas 2 were in the “Down with Cover” forage guild and 2 were in the “No Pattern” forage guild.

Table 3. Two-dimensional guild membership in Sierran mixed conifer habitat for 8 common prey[a] of the northern goshawk as reported by Bloom et al. (1985).

Species[b]	Reproductive guild	Cover guild	Forage guild
Birds			
American robin	US_DC [c]	US_DC	DC
Blue grouse	US	US	US
Northern flicker	US	US	NP
Steller’s jay	USC	US	NP
Mammals			
Douglas’ squirrel	USC	USC	US
Golden-mantled ground squirrel	DC	DC	DC
Northern flying squirrel	USC	USC	USC
Western gray squirrel	US	US	US

[a] The criterion for choosing 8 species was that each accounted for at least either 5% of prey individuals or 5% of total prey biomass from the study. An additional 2 species that met this criterion are not included here because they did not meet the moderate or high habitat suitability threshold in HUGS.

[b] Scientific names of species in the table that are not mentioned in the text are blue grouse (*Dendragrapus obscurus*), Steller’s jay (*Cyanocitta stelleri*), Douglas’ squirrel (*Tamiasciurus douglasii*), golden-mantled ground squirrel (*Spermophilus lateralis*), northern flying squirrel (*Glaucomys sabrinus*), and western gray squirrel (*Sciurus griseus*).

[c] Guild abbreviations are “Up with Size” (US), “Down with Cover” (DC), “Up Size and Cover” (USC), “Up Size Down Cover” (US_DC) and “No Pattern” (NP).

DISCUSSION

Assessing the value of HUGS begins with an understanding of how biological models are developed and used. Biologists use many types of wildlife models that range from single-species models that employ multivariate statistical analysis and habitat suitability indices to multispecies models including ecosystem simulation and hierarchy models (Morrison et al. 1998). Using this terminology, the CWHR

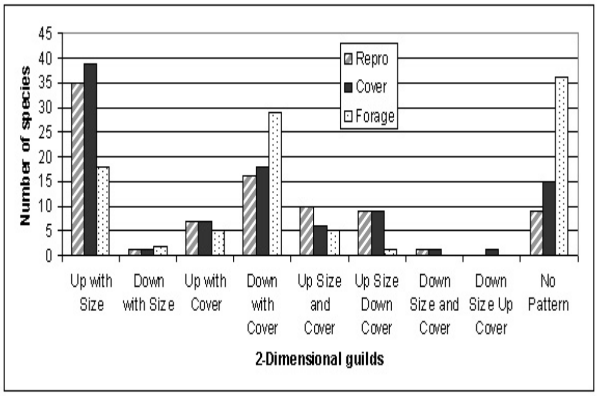

Fig. 5. Two-dimensional Habitat Utilization Guilds Software guilds for birds predicted to occur in Sierran mixed conifer habitats at moderate and high suitability ratings from the California Wildlife Habitat Relationships system.

system, on which HUGS is based, is a multispecies model composed of numerous species–habitat matrices. The CWHR model and its matrices were developed using a combination of published literature and expert opinion (Airola 1988). Although CWHR was not directly developed from empirical field data, numerous validation studies of the CWHR models have been undertaken for various habitats and wildlife taxa (Garrison 1993, Barrett and White 1999) and this information has been used periodically to update the models (Garrison et al. 2000). Despite the continuous improvement provided by validation studies, the usefulness of both CWHR and HUGS must be qualified by a statement that neither model includes explicit provisions for addressing spatial issues, such as juxtaposition of habitats or minimum functional patch size (Airola 1988). In addition, the CWHR habitat classification classes are better suited to describing even-aged forest stands than uneven-aged stands, such as those commonly found in selectively logged Sierran mixed conifer and eastside pine forests. On the other hand, the rate of commission and omission errors for species prediction is likely to be much higher at smaller scales (Raphael and Marcot 1986, Edwards et al. 1996,). Consequently, we maintain that HUGS is a valuable tool when applied at the scale of landscape or regional forest type.

The usefulness of HUGS is also related to how well it assigns species to guilds meaningful to scientists, resource managers, and decision makers. To this end, we have looked at several published lists itemizing wildlife species with habitat preferences comparable to the response patterns identified by HUGS. For example, in its Coniferous Forest Bird Conservation Plan, the California Partners in Flight (2002:27) identified 7 avian focal species—the marbled murrelet (*Brachyramphus marmoratus*), spotted owl, gray jay (*Perisoreus canadensis*), golden-crowned kinglet (*Regulus satrapa*), brown creeper (*Certhia americana*), pileated woodpecker, and great gray owl (*Strix nebulosa*)—threatened because of loss of old-growth coniferous forest habitat. Interestingly, HUGS assigned all of these species to the most closely corresponding "Up Size and Cover" and "Up with Size" 2-dimensional guilds. In addition, as part of the Sierra Nevada Forest Plan Amendment, the U.S. Forest Service (2004) adopted 43 management indicator species (MIS) for evaluating the effects of proposed management activities. Of the 9 MIS associated with mature conifer habitat by the U.S. Forest Service (2004), HUGS assigned 7 species to the most closely corresponding "Up Size and Cover" or "Up with Size" reproductive and cover 2-dimensional guilds. These species were the pileated woodpecker, black bear (*Ursus americanus*), Douglas' squirrel, northern flying squirrel, golden-crowned kinglet, rubber boa (*Charina bottae*), and western gray squirrel. Of the 7 MIS linked to early seral forest or forest openings by the U.S. Forest Service (2004), HUGS assigned 6 species—the calliope hummingbird, wild turkey (*Meleagris gallopavo*), elk (*Cervus elaphus*), mule deer (*Odocoileus hemionus*), dusky-footed woodrat (*Neotoma fuscipes*), and western skink (*Eumeces skiltonianus*)—to the most closely corresponding "Down with Cover" and "Down Size and Cover" foraging 2-dimensional guilds. Finally, Thomas (1979) developed a list of life forms for the Blue Mountains of Oregon and Washington that include many of the same groupings predicted by HUGS. We reason that some of these life forms are comparable to HUGS guilds because the species in these life forms that occur within forested habitats in the

Blue Mountains are similar to those found in California. One of these life forms was for animals that reproduce on very thick branches and feed on the ground. It comprises 7 bird species: great blue heron (*Ardea herodias*), red-tailed hawk, golden eagle, bald eagle (*Haliaeetus leucocephalus*), osprey, great horned owl (*Bubo virginianus*), and great gray owl. HUGS assigned 5 of these species to the most closely corresponding "Up with Size" 1-dimensional reproductive guild. To the most closely corresponding "Down with Cover" and "No Cover Pattern" 1-dimensional foraging guilds, HUGS assigned 2 and 4 species, respectively.

The 3 comparisons enumerated above suggest that HUGS guild assignment corresponds reasonably well to at least some species of management concern in California, Oregon, and Washington. The model appears to work better with respect to tree size than with canopy cover based on these comparisons. One reason for this discrepancy is that HUGS does not explicitly address herbaceous and shrub-dominated habitats. Although the "Down with Cover" guild often includes species associated with shrub and herbaceous habitat elements found in open forest conditions, HUGS does not always count some wildlife taxa (e.g., *Microtus* spp.) associated with small patches of nonforest habitat (e.g., wet meadow, chaparral) within a forested landscape

The Sierran mixed conifer 1-dimensional and 2-dimensional modeling results demonstrated earlier (Figs. 4 and 5) highlight some intriguing relationships between biodiversity and habitat structure. The modeling results show that a high proportion of bird species was associated with large tree diameters with respect to reproductive and cover habitat, whereas a high proportion of bird species was also associated with open forest canopy with respect to forage habitat. This result is not surprising; it is consistent with ecological theory that forest biodiversity is highest at either end of the successional spectrum (Bormann and Likens 1979). At 1 end, structurally complex, large-diameter trees provide nesting and cover substrate for many birds. At the other end, less area occupied by conifers leaves more growing space for herbaceous plants, shrubs, and deciduous trees that provide foraging habitat for many birds and the insects on which some birds feed. The modeling results also reveal that there are 2 smaller, but ecologically important, guilds that have different trajectories toward late-seral forest conditions. The "Up Size and Cover" guild, including spotted owl, northern goshawk, and pileated woodpecker, encompasses the classic conception of closed-canopy, late-seral forest habitat. On the other hand, the "Up Size Down Cover" guild, including purple martin, red-breasted sapsucker, and western bluebird, utilizes late-seral forest characterized by open canopy conditions or numerous gaps and edges. No-pattern guilds contain the largest number of species, particularly with respect to tree size and forage. This suggests that tree size is less important than other habitat elements with respect to the suitability of forage habitat for many animals. Another explanation is that some animals are generalists with respect to tree size and canopy cover conditions, or rely on habitat elements not addressed in HUGS, such as edge, riparian vegetation, and oak trees.

With respect to prey of the northern goshawk, we noted that HUGS results suggest that, whereas all prey species except golden-mantled ground squirrel were associated with large trees for reproduction, there was a split between large tree specialization, ground story specialization, and generalist behavior when it came to classifying the feeding habits of these species (Table 3).

MANAGEMENT IMPLICATIONS

There has been a moderate amount of interest in HUGS by various parties. The DFG has used guild lists generated by HUGS to support cumulative impact assessments and mitigation recommendations for timber harvesting plans in Trinity and Humboldt counties. The DFG has also used HUGS in conceptual area plans to demonstrate the value of conservation easements. The California Department of Forestry and Fire Protection has used HUGS in forest planning on state lands. The Lassen National Forest has used HUGS to support habitat restoration projects. In addition, 1 consulting firm has used HUGS in the development of watershed assessment reports. Furthermore, faculty and researchers at Humboldt State University, Shasta College, and the University of California at Davis have requested information on HUGS.

In conclusion, with more use and evaluation, HUGS may prove a useful tool for elucidating patterns between biodiversity and the mosaic of habitats occurring at a landscape scale in California forests and woodlands. HUGS may be especially valuable for clarifying general landscape effects of habitat changes on large groups of species, instead of the traditional focus on smaller scale impacts on a narrow set of special-status or indicator species. However, additional tools including spatial and temporal modeling, will be required to answer more complex questions about cumulative impacts, thresholds of significance, and the desired mix of habitats for maintaining a diversity of wildlife in forest and woodland landscapes.

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