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Quantitative snag targets for the three-toed woodpecker *Picoides tridactylus*

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Sustainable forest management goals include the conservation of biological diversity and its constituent elements. Dying and dead trees, in particular, have been recognised as being of prime importance as resource and habitat for numerous animal and plant species. Nevertheless, few quantitative target values have been defined for dead wood management purposes, and they often lack well-founded scientific bases.

In this study we developed such quantitative targets for standing dying and dead trees (defined as snags), based on the habitat requirements of the three-toed woodpecker *Picoides tridactylus*, a keystone species whose presence is considered an indicator of the properties of naturally dynamic forests. First we developed a theoretical model based on energy requirements and with predictions for woodpecker breeding probabilities as a function of available snag quantities. Then an empirical field study was conducted in Switzerland with the aim of verifying the model predictions. For this purpose, 12 pairs of sites of 1 km^2 in size and comprising one site with and one without a breeding woodpecker, were sampled for snags. We compared these sites using logistic regression. Finally, the comparison of the theoretical model with the field approach enabled the derivation of quantitative snag targets for spruce forests.

Both our theoretical model and the logistic regression analyses resulted in similar snag quantities for predicted woodpecker occurrence. For management purposes, we recommend the observation of the precautionary principle by striving for target values of 1.6 m^2 ha^{-1} (basal area) or 18 m^3 ha^{-1} (volume) or 14 (dbh $\geq$ 21 cm) snags per hectare in an area of 100 ha, corresponding to a probability of $\geq$ 0.9 for woodpecker occurrence in both approaches. Maintaining or achieving such optimal snag levels allows the local persistence of three-toed woodpeckers in forest patches and may serve to define strategies for the maintenance of local populations.

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The conservation of biodiversity has become one of the key goals of sustainable forest management (Lindenmayer et al. 2000). At a certain level of forest management intensity, the lack of habitat components causes once naturally occurring species to decline to the level where they risk extinction. Habitat destruction and degradation is currently considered as the major cause of species extinction (e.g., Tilman et al. 1994, Dobson et al. 1997, Fahrig

2001). In Switzerland, for example, in addition to selective logging of large trees, diseased and dead trees are often systematically removed for sanitary reasons by means of salvage cutting (Guby and Dobbertin 1996) causing a lack of habitats and resources for species that depend on dead wood. Quantitative target values may be derived from reference systems, such as naturally dynamic forests, with the aim of restoring dead wood and other important habitat components in managed forests. However, none or very few natural forests remain in most parts of Europe. Also, the amount of dead wood in natural forests may be so extensive – up to 30% of dead stems (Linder et al. 1997) or 25% of above ground biomass (Siitonen 2001, Nilsson et al. 2002, Bobiec in press) – that such targets would be incompatible with the economic objectives of multifunctional forestry. Another approach involves the quantification of the ecological preferences of species of special interest and derivation of quantitative target values for use in management (Simberloff 1995, With and Crist 1995, Fahrig 2001). One difficulty here, however, is the definition of species of special interest and justification of their role as biodiversity surrogates (Thompson and Angelstam 1999). The use of the keystone, indicator, focal and umbrella species concepts (Pearson 1994, Lambeck 1997, Simberloff 1998, Fleishman et al. 2000) for management considerations is currently increasing, in spite of many remaining scientific uncertainties in relation to certain species being appropriate proxies for others (Lindenmayer et al. 2000).

Among vertebrates, woodpeckers are of special importance due to their key role in supplying forests with tree-cavities, serving secondary users as nesting or roosting holes (Saari and Mikusiński 1996). In terms of their ecological requirements, woodpeckers are considered as being the most demanding guild among resident bird species (Angelstam 1990, Mikusiński and Angelstam 1997). The occurrence of several species of woodpeckers is indicative of the properties of naturally dynamic forests (e.g. old trees, dead wood, structural diversity) (Mikusiński and Angelstam 1997). The three-toed woodpecker *Picoides tridactylus*, in particular, has recently been proposed as a keystone species (Imbeau 2001) and a possible indicator of high biodiversity, i.e. old trees and large dead trees (Mikusiński et al. 2001, Nilsson et al. 2001).

One of the most important habitat features for three-toed woodpeckers are large, standing dying and recently dead trees (Hogstad 1970, Hess 1983, Pechacek 1995, Murphy and Lehnhausen 1998, Ruge et al. 1999b). Such dead wood pieces are the rarest of the diverse dead wood substrata, especially in managed forests (Green and Peterken 1997, Fridman and Walheim 2000). They still have a certain economic value and may, therefore, be cut when timber is harvested. Ecological studies on dead wood have demonstrated the prime importance of large diameters and standing compared to lying dead trees (Samuelsson et al. 1994). They provide habitats and resources for numerous threatened animal, plant and fungal species (Thomas 1979, Utschick 1991, Morrison and Raphael 1993, Samuelsson et al. 1994, Smith 1997, Jonsson and Kruys 2001). Recently, dead wood has been proposed as a new indicator of forest biodiversity to be approved by the Fourth Ministerial Conference on the Protection of Forests in Europe in 2003 (<www.minconf-forests.net> 29 April 2002). Dead wood also figures in modern certification standards for best forestry practices, as defined, for example, by the Forest Stewardship Council (FSC). With its requirement of forests with relatively high dead wood amounts (Derleth et al. 2000) and demonstration of threshold responses related to dead wood (Bütler et al. unpubl.), the three-toed woodpecker is directly linked with the structure-based biodiversity indicator "dead wood".

In spite of the growing agreement between conservation biologists, forest managers and political circles on the importance of dying and dead trees, the few existing quantitative dead wood management targets for European forests often lack well-founded scientific bases. Without sound quantitative targets, however, the achievement of management goals and progress towards sustainable forestry cannot be assessed. Due to its specific requirements for standing dying and dead trees (defined as snags), and due to its qualities as a keystone species and biodiversity indicator, the three-toed woodpecker was used in this study to define quantitative snag target values for sustainable management of spruce forests. The aims of this paper are: 1) to develop and validate a theoretical model based on the energy budgets of the three-toed woodpecker, thus predicting the spatial densities of snags required to meet this woodpecker's energy requirements; 2) to test these predictions by carrying out a subsequent field study and 3) to derive quantitative management recommendations through the definition of snag target values.

Methods

The probability of presence of the three-toed woodpecker *Picoides tridactylus* was predicted as a function of the snag density (SNAG) by developing a simple model based on the energy requirements of the three-toed woodpecker, and on different assumptions with respect to food selection and prey availability. After a sensitivity analysis, this theoretical model was validated on ten study sites in Switzerland. In order to verify the model predictions concerning snags, a field study, aimed at measuring the quantities of snags actually available in sites where three-toed woodpeckers do and do not breed, was subsequently carried out at 24 sites. A logistic regression analysis on the "presence – absence" data in these sites also resulted in a prediction of the probability of woodpecker presence as a function of the snag density. Through comparison of both probability predictions, quantitative snag target values were then derived for this woodpecker species.

The bioenergetic model

The basic idea behind our model is that a three-toed woodpecker breeding pair has to find sufficient energy sources within its home-range so as to fuel all its activities over the course of one year (reproduction, moulting, overwintering etc). According to Glutz von Blotzheim (1994), the mean reproduction of a successfully breeding pair is 1.8 young birds. Such a bird group (2 adults and 1.8 young) is defined as a family. Thus, we included in our model the energy needs of the young birds over 14 weeks, after which they are supposed to leave the home-range definitely. Following Hess (1983) we defined the number per area unit of foraging trees as the most important habitat feature, while regarding the availability of trees for nesting, drumming etc as not being limiting factors. For practical management considerations, the density of all snags, and not only potential foraging trees, was defined as key variable in the model (Fig. 1). As an insectivorous bird, the three-toed woodpecker gains its energy through insect predation. According to the literature, bark beetles (above all *Ips typographus*) were considered as the most important energy source (Hutchinson 1951 in Baldwin 1968, Hogstad 1970, Sevastjanow 1959 in Scherzinger 1982, Hess 1983, Pechacek and Kristin 1993, Formosow et al. 1950 in Glutz von Blotzheim 1994). Bark beetles occur only in a certain phase in the gradual change in the properties of a dying and dead tree. Hence, only a given proportion (b) of snags, trees which have still some bark left, are potential foraging trees. Koplin (1972) estimated the daily energy requirements of free-living three-toed woodpeckers by measuring gross energy intake and energy in excrement. In his model, the energetic requirement is a function of air temperature, considered as the most important metabolic factor. This model served as basis for the estimation of the yearly energy requirements of woodpeckers in our model, defined as the number of consumed prey during one year (CPR). As a substitute for lacking data on movements and energy expenditure by woodpeckers, we used the potential home-range size (PHR), defined as a home-range within a minimum and maximum size, facilitating the viability of the woodpecker family. The size range was based on home-range sizes reported in the literature.

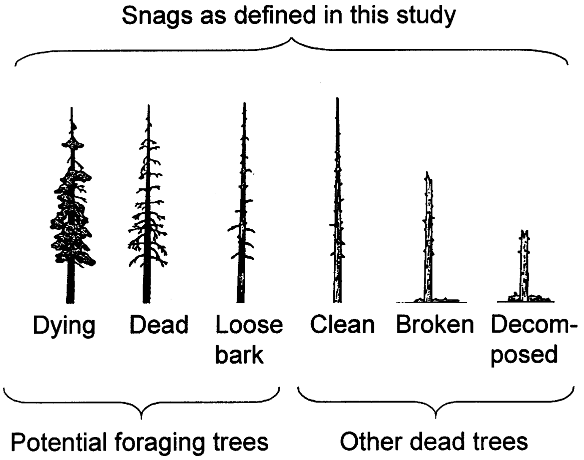

Fig. 1. Definition of snags and potential foraging trees for the three-toed woodpecker, as used in this study. Modified from Thomas (1979).

The available prey number (APR) of the most important energy source, i.e. bark beetles, was estimated on the basis of reproduction and mortality rates from the literature (cf. variable estimation). Since bark beetles live beneath the tree bark, the mean bark area infested by beetles (MIA) was a further variable included in the model. Finally, we defined the woodpecker's foraging efficiency (FEF) as a variable that takes into account a certain loss of prey during foraging. Indeed, even when virtually scaling the bark of a foraging tree, the woodpecker will not capture all available prey items, since bark chips that fall to the ground may contain undetected items. In addition, other insectivores may consume bark-living insects.

Based on the above considerations, the snag density needed to meet the woodpecker's energy requirements can be estimated by calculating:

$$\mathrm{SNAG}_{21} = \frac{\mathrm{CPR}}{b \times \mathrm{PHR} \times \mathrm{APR} \times \mathrm{MIA} \times \mathrm{FEF}} \tag{1}$$

where: SNAG_{21} = density of snags with a diameter at 1.3 m (dbh) ≥ 21 cm (cf. validation of the bioenergetic model) required to meet the annual energy requirements of a woodpecker family [snags $\times$ ha^{-1}], CPR = bark beetle prey consumed in the course of one year by a woodpecker family [consumed beetles $\times$ yr^{-1}], PHR = potential home-range size of a woodpecker breeding pair [ha], APR = available prey over one year per square meter of bark on potential foraging trees in the woodpecker's home-range area [available beetles $\times$ m^{-2} $\times$ yr^{-1}], MIA = mean infested bark area of a potential foraging tree [m^2 $\times$ foraging tree^{-1}], FEF = foraging efficiency of an adult woodpecker [consumed beetles $\times$ available beetles^{-1}], b = proportion of potential foraging trees to all snags [foraging trees $\times$ snags^{-1}].

Since a woodpecker breeding pair consists of two adult birds and is supposed to produce 1.8 young birds annually, CPR is further defined by

$$\mathrm{CPR} = 2 \times \mathrm{CPR}_a + 1.8 \times \mathrm{CPR}_y \tag{2}$$

where: CPR_a = bark beetle prey consumed over one year by 1 adult woodpecker, CPR_y = bark beetle prey consumed over 14 weeks by 1 young bird.

CPR_a is further defined by

$$\mathrm{CPR}_a = \sum_{i=1}^{12} 30 \times \frac{\mathrm{GEI}(T_i)}{e} \times p_a \tag{3}$$

where: GEI = gross energy intake in Joule per day = (51.46 – 0.67 $\times$ T_i) $\times$ 4185 J, according to Koplin (1972), T_i = mean monthly temperature in °C, e = energy content in

Joule of 1 bark beetle item, p_a = proportion of bark beetles in the diet of an adult woodpecker.

CPR_y is further defined by

$$CPR_y = \sum_{j=1}^{14} 7 \times \frac{BW(j) \times p_y(j) \times p(BW)}{w_f} \qquad (4)$$

where: BW(j) = body weight in week j (g), p_y (j) = proportion of bark beetles in the diet of a young bird in week j, p(BW) = proportion of body weight a young bird is eating per day, w_f = fresh weight of a bark beetle larva or adult (g).

APR is further defined by

$$APR = \frac{1}{52} \times a \times n_a \times \sum_{j=1}^{52} 1 - m(j) \qquad (5)$$

where: a = bark beetle attack density, i.e. the number of nuptial chambers per square meter of bark (m^{-2}), n_a = mean number of eggs per nuptial chamber, m(j) = cumulative mortality rate of eggs, larvae, pupae, imagos, immature and adult beetles in week j.

Variable estimation

CPR

In order to estimate the consumed prey CPR we assumed a moisture content of 70% for *Ips typographus* larvae or adults (Bell 1990), a mean caloric content of 83.7 J for one item (Koplin 1972, Barbault 1997) and a dry weight w_d of 0.0041 g (Wermelinger pers. comm.) and, thus, fresh weight $w_f = w_d/0.3$. Following Koplin's GEI-model, at 0°C an adult woodpecker was supposed to consume prey whose fresh weight represents ca 0.5 times the woodpecker's body weight. Based on the consideration of the data available on bird digestion (Karasov 1990) and energy requirements for different bird sizes (Kendeigh 1970), this appeared to be a realistic winter daily diet for an insectivorous bird. The proportion of bark beetles in the diet of an adult woodpecker p_a was assumed to be 0.75 (Hutchinson 1951 in Baldwin 1968, Hogstad 1970, Sevastjanow 1959 in Scherzinger 1982, Hess 1983, Pechacek and Kristin 1993, Formosow et al. 1950 in Glutz von Blotzheim 1994).

The body weight in week j BW(j) of young woodpeckers was estimated according to the growth curve of Pechacek and Kristin (1996), in which the body weight is 20 g in the first week, 50 g in the second week and 65 g from the third week on. Since the nestlings' growth is fast and the energy cost of growth is high, and considering data for other bird species (Westerterp 1973), we assumed that a young bird consumes 0.7 times its body weight per day. The proportion of bark beetles in the diet of a young bird in week j $p_y(j)$ was defined as 5.8% during weeks 1–3 (Pechacek and Kristin 1996), 10% in week 4, 20% in week 5, 30% in week 6, 50% in week 7 and 75% from week 8 on.

Based on the above assumptions and on mean monthly temperatures T_i between –6 and +12°C, the estimated CPR varied between 1.605×10^6 and 1.623×10^6 bark beetle items per year (Table 1). Its probability distribution was assumed to be uniform (cf. Monte Carlo simulation).

PHR

The potential home-range size PHR was assumed to vary uniformly between 44 and 176 ha, corresponding to the maximum and minimum home-range size reported in the literature for *Picoides tridactylus alpinus* (Bürkli et al. 1975, Scherzinger 1982, Hess 1983, Pechacek 1995, Dorka 1996, Pechacek et al. 1999, Ruge et al. 1999b).

APR

The breeding density of *Ips typographus* is highly variable within a tree, among trees and at different bark beetle population levels (endemic to epidemic). Our estimation was based on data for endemic (no outbreak) population levels in natural sub-Alpine spruce forests. Only one beetle generation per season was expected and the egg laying was set to the second week of June (Nierhaus-Wunderwald 1995). With an attack density (a) of 150 nuptial chambers m^{-2} (Weslien and Regnander 1990) we expected an average n_a of 27 eggs per nuptial chamber (Thalenhorst 1958). The duration of the development cycle was defined as 3 weeks for eggs, 3 weeks for larval stage and 6 weeks for pupal and imago stage. The mortality rate m(j) in week j was expected to be linear during each development stage and to reach

Table 1. Probability distribution functions defined for the variables in the bioenergetic model used to estimate the density of dying and dead trees required to meet the three-toed woodpecker's energy needs.

Variable [unit]	Type of distribution	x_{min}/x_{max}	μ/σ [1]	x_a/x_b [2]
PHR [ha]	uniform	44/176		
APR [m^{-2}]	normal		657/±216	234/1080
FEF [percent]	normal		0.50/±0.13	0.25/0.75
MIA [m^2]	normal		12.5/±3.8	5/20
CPR [number]	uniform	$1.605 \times 10^6/1.623 \times 10^6$		

[1] μ = mean; σ = standard deviation.

[2] $P(x_a < Z < x_b) = 0.95$.

25% of the initial population in week 3, 70% in week 6 and 85% in week 12 (Thalenhorst 1958, Balazy 1968). During the 40 weeks of maturate feeding, hibernating, flight and invasion on new trees, another linear mortality of 50% of the individuals that reached full development was expected.

Based on the above assumptions, we estimated the APR as 657 ± 216 (mean ± SD) and normally distributed within $x_a = 234$ and $x_b = 1080$ ($Pr(x_a < Z < x_b) = 0.95$); cf. Monte Carlo simulation.

MIA

Very little data exists on the proportion of spruce tree bark area, MIA, infested by *Ips typographus*. Gonzalez et al. (1996) reported a MIA of 21 m^2 for spruce trees with a mean dbh of 46 cm for an endemic population level. Weslien (1990) indicated attacks of 50% of the tree height for spruce trees with a mean dbh of 30 cm.

Based on Gonzalez et al. (1996) and Weslien and Regnander (1990) and our own data on the diameter frequency distributions of spruce trees (Bütler unpubl.), we estimated the MIA as 12.5 ± 3.8 m^2 (mean ± SD) and normally distributed within $x_a = 5$ and $x_b = 20$ ($Pr(x_a < Z < x_b) = 0.95$); cf. Monte Carlo simulation.

FEF

Capture rates of insect prey vary seasonally, mainly in relation to weather (Wolda 1990). No data was found on the foraging efficiency of bark beetle predation by woodpeckers. Bark chips removed by the woodpecker fall to the ground and may contain bark beetle items that are not consumed. Based on Baldwin (1968), we estimated the FEF as normally distributed with 0.50 ± 0.13 (mean ± SD) within $x_a = 0.25$ and $x_b = 0.75$ ($Pr(x_a < Z < x_b) = 0.95$); cf. Monte Carlo simulation.

b

The proportion of potential foraging trees to all snags (b) was determined by field measurements of randomly selected snags (N = 1392) at six study sites (Bütler unpubl.). The decomposition stage of each tree was determined using the method described in Thomas (1979). Only trees with the decomposition stages "dying", "dead" and "loose bark" were considered as potential foraging trees (Fig. 1). As we observed small variations of b between the six study sites, we defined it as a constant (b = 0.8).

Monte Carlo simulation and sensitivity analysis

The input variables (CPR, PHR, APR, MIA and FEF) do not have one determined value, but are defined as independent random variables. In order to calculate the outcome variable $SNAG_{21}$, we undertook a random experiment by means of ten Monte Carlo simulations, based on a sample size of N = 10000 for each input variable. The variables PHR and CPR were supposed to have a uniform probability distribution. The largest and smallest home-range sizes reported in the literature for European three-toed woodpeckers were used to define the upper and lower limits x_{max} and x_{min} for PHR (Bürkli et al. 1975, Scherzinger 1982, Hess 1983, Pechacek 1995, Dorka 1996, Pechacek et al. 1999, Ruge et al. 1999a). For *CPR*, the definition of x_{max}/x_{min} was based on lowest/highest monthly mean temperatures within the range of the three-toed woodpecker's geographic distribution. We assumed a normal distribution for the variables APR, MIA and FEF. The mean values of the variables related to bark beetle infestation (APR, MIA) corresponded to an endemic bark beetle population level (cf. Table 1). Ecologically relevant limits x_a and x_b were chosen in such a way as to obtain 95% of the values within those limits, and the corresponding standard deviations were then calculated. Finally, we plotted the probability density function of the simulated output random variable $SNAG_{21}$ and its cumulative distribution function.

The parameter estimation of the input variables (x_{min}, x_{max}, x_a, x_b, mean and standard deviation) for the model variables is subject to uncertainties. A sensitivity analysis changing each variable in turn by ± 20% revealed the extent of changes of the predicted SNAG-value. A simultaneous change of ± 20% for all variables was undertaken to demonstrate an extreme situation.

Validation of the bioenergetic model

The bioenergetic model was validated at 10 study sites in Switzerland, where the three-toed woodpecker was present (n = 6) and absent (n = 4), respectively. Woodpecker presence was determined by visual and aural detection and fresh foraging signs. All of the study sites were dominated by sub-Alpine spruce forests and the surveyed areas varied between 0.6 and 3.0 km^2. The snags were measured at each site using a recently developed method that is further described elsewhere (Bütler and Schlaepfer unpubl.). This method quantifies snags by coupling remote sensing techniques with a Geographic Information System. The dbh of snags that can be quantified by this method is ≥ 21 cm. With the model eq. (1), and with the defined probability distribution functions as input values (Table 1), the p-value (probability of woodpecker presence) associated to each measured $SNAG_{21}$-value was then calculated and compared with information on the presence/absence of the woodpecker.

Study sites and design for the empirical model

The field study was conducted between 1998 and 2001 at 24 sites located in Switzerland in the eastern/central and western Pre-Alps and in the Jura Mountains. Regional pairs of field plots of 1 km^2 in size were selected (2 × 12 units). Each pair of plots consisted of one plot where the three-toed woodpecker was present during the breeding season of the study years (referred to as "presence") and one where it has never been observed (referred to as "absence"). Breeding was proven for three plots, whereas it was probable for the others, according to the definition in the International Ornithological Atlases (Sharrock 1973). The selection of presence/absence field plots was based on data provided by the Swiss ornithological station of Sempach (cf. Schmid et al. 1998) and local bird watchers in Switzerland, and was subject to the following criteria: a) spruce tree dominated forests; b) the majority of the forest stands > 100 yr old, i.e. mature to over-mature, the stand age preferred by three-toed woodpeckers; c) between 1200 and 1700 m a.s.l., where the probability of three-toed woodpecker occurrence is highest (cf. Schmid et al. 1998).

In each field plot, a 4 × 4 sampling grid was established, with sampling points 250 m apart.

Data gathering and statistical analysis

Data was collected by fieldwork at the sampling points using angle relascope, clinometer and compass. The minimal inventory diameter for snags was 10 cm dbh ($SNAG_{10}$) and their minimum height 6 m. The number of trees being wider than the gap in the relascope at each point represented the basal area (i.e. the area of the cross section of a tree stem at 1.3 m inclusive of bark; m^2 ha^{-1}) of the forest at the sampling point.

For statistical analyses we used the STATISTICA 6.0 software package. The mean basal area of $SNAG_{10}$ at the sampling points was calculated for each field plot. The plots were then separated into two groups ("presence" and "absence") and group means and ranges were calculated. We checked for between-group differences by calculating t-statistics. Logistic regression (Hosmer and Lemeshow 1989) was chosen as the appropriate method to predict the probability of the presence or absence (coded as 1 and 0) of three-toed woodpeckers as a function of the $SNAG_{10}$-densities.

Results

The bioenergetic model and its validation

The simulated model solution predicted a probability of <50% for presence of the three-toed woodpecker, if the density of standing $SNAG_{21}$ (dbh ≥ 21 cm) is less than five trees per hectare (Fig. 2). For densities rising from five to fourteen trees, the expected probability increased from 50 to 90%.

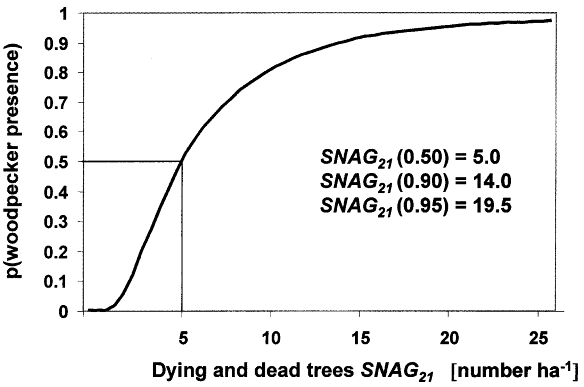

Fig. 2. Simulated solution of the bioenergetic model predicting the probability of three-toed woodpecker presence as a function of the density of dying and dead trees with a dbh ≥ 21 cm.

The results of the sensitivity analysis (Table 2) show the deviation of the $SNAG_{21}$-values (for p(woodpecker presence) = 0.5) due to changes of ± 20%, in turn, of each input variable. The original $SNAG_{21}$-value ($p = 0.5$) was 5.0. Deviations of the output $SNAG_{21}$-value varied between –0.9 and +1.5. For example, changing the number of consumed prey CPR by + 20% (i.e. assuming lower air temperatures), increased the required $SNAG_{21}$-density from 5.0 to 6.2 trees ha^{-1}. Positive shifts in $SNAG_{21}$-values were always larger than negative shifts.

The validation of the model resulted in predicted probabilities of three-toed woodpecker presence ≥ 0.2 for sites where the species was actually present and $p < 0.05$ for those where it was absent (Table 3).

Results of the empirical model

The mean basal area of $SNAG_{10}$ showed significant differences between the one km^2 field plots with and without woodpeckers. For "presence" plots we obtained 2.3 (0.6–6.0) m^2 ha^{-1} (mean; range) and for "absence" plots 0.4 (0.0–0.8) m^2 ha^{-1} (DF = 22, t = 4.37, p = 0.0002).

Indeed, the probability of woodpecker presence increased significantly with $SNAG_{10}$ (Fig. 3; $\chi^2 = 25.04$, $p < 0.000$, DF = 1). In this empirical model the probability of three-toed woodpecker presence increased from 0.10 to 0.95 when the basal area of $SNAG_{10}$ rose from 0.6 to 1.3 m^2 ha^{-1}.

Comparison of the bioenergetic with the empirical model

In order to compare the results of the bioenergetic model with those of the field study, a data transformation was necessary, since both the measurement units and minimum dbh for snags differed. For this transformation we

Table 2. Sensitivity analysis for the output value of the bioenergetic model: changes in predicted SNAG_{21}-values for p(woodpecker presence) = 0.5 after 20% changes of input variables.

Changed variable	New SNAG_{21} *) (+Δ)	New SNAG_{21} (–Δ)	Deviation x)
CPR	6.2	4.1	–0.9 to +1.2
PHR	4.3	6.5	–0.7 to +1.5
APR	4.2	6.4	–0.8 to +1.4
MIA	4.3	6.5	–0.7 to +1.5
FEF	4.2	6.5	–0.8 to +1.5
CPR, PHR, APR, MIA, FEF	2.9	10.3	–2.1 to +5.3

*) Original SNAG_{21}-value for p(woodpecker presence) = 0.5 was 5.0.

x) Deviation is the change in predicted upper and lower limits for the SNAG_{21}-value.

used an experimental curve of tree diameter distributions from field data from six study sites (Bütler unpubl.; Fig. 4). The predicted SNAG_{21}-value, given as tree density ($\text{n ha}^{-1}{}_{\geq 21\text{ cm}}$), was translated into stand basal area ($\text{m}^2\ \text{ha}^{-1}{}_{\geq 10\text{ cm}}$) in two steps:

$$1)\quad \left[\text{n ha}^{-1}{}_{\geq 21\text{ cm}}\right] \times \text{TBA}_{\overline{\text{dbh}}} = \left[\text{m}^2\ \text{ha}^{-1}{}_{\geq 21\text{ cm}}\right]$$

with: TBA = tree basal area [m^2] = $(0.5\ \text{dbh})^2 \times \pi$, $\text{TBA}_{\overline{\text{dbh}}}$ = tree basal area of the mean-sized tree with a dbh ≥ 21 cm.

$$2)\quad \left[\text{m}^2\ \text{ha}^{-1}{}_{\geq 21\text{ cm}}\right] \times \frac{1}{p_{\geq 21\text{ cm}}} = \left[\text{m}^2\ \text{ha}^{-1}{}_{\geq 10\text{ cm}}\right]$$

with: $p_{\geq 21}$ = proportion of total basal area of trees with a dbh ≥ 21 cm. The mean-sized tree with a dbh ≥ 21 cm was 33.5 ± 12.1 cm (mean ± standard deviation; N = 485), corresponding to a $\text{TBA}_{\overline{\text{dbh}}}$ of 0.09 m^2. The resulting $p_{\geq 21}$ was 0.77.

Figure 5 and Table 4 show the direct comparison between the solution of the bioenergetic model and the results of the logistic regression. Both probability functions lie close together, in particular for p(woodpecker presence) between 0.7 and 0.8. A SNAG_{10}-density of < 0.6 $\text{m}^2\ \text{ha}^{-1}$, i.e. p(woodpecker presence) < 0.5 in both, theoretical modelling and empirical field approaches, is considered as unfavourable for the woodpecker, whereas a density in excess of 0.9 $\text{m}^2\ \text{ha}^{-1}$, i.e. p(woodpecker presence) > 0.5 in both approaches, is considered as favourable.

Discussion

In North America, some land-management agencies have defined standards requiring the retention of specified numbers and kinds of snags to provide habitats for wildlife. For ponderosa pine *Pinus ponderosa* and mixed-conifer

Table 3. Validation of the bioenergetic model for 10 study sites. The SNAG_{21}-value was measured for each study site and the associated p-value calculated with the bioenergetic model equation and the defined probability distribution functions (Table 1) as input values.

	SNAG_{21} [n ha^{-1}] *)	P(woodpecker) x)
Site with three-toed woodpecker		
Hobacher	7.1	0.7
Hinteregg	11.2	0.8
Bärenegg	10.7	0.8
Hinterberg	2.9	0.2
Bois des Fayes	4.5	0.4
Bödmeren	3.4	0.3
Site without three-toed woodpecker		
Langenegg	1.5	< 0.02
Mont Pelé	1.9	< 0.05
Schraewald	1.2	< 0.01
Les Arses	0.8	< 0.01

*) measured SNAG_{21}-value.

x) predicted probability of three-toed woodpecker presence by the bioenergetic model.

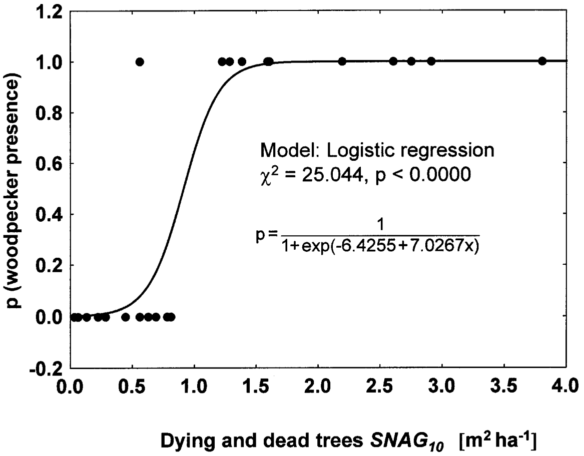

Fig. 3. Logistic regression model showing a significant relationship between the stand basal area of dying and dead trees and the probability of three-toed woodpecker presence.

forests, for example, US Forest Service recommendations call for retention of 4.9 and 7.4 snags ha^{-1} with a minimum dbh of 46 cm and minimum height of 9 m (Ganey 1999). This author demonstrated, however, that these snag standards were seldom met even in unlogged forests and concluded that current standards may be unrealistic and should be reconsidered. One reason is that no solid scientific basis was provided for the recommended snag densities, thus highlighting the great need for additional work in these areas. The lack of scientific bases would also appear evident for European forest standards, as illustrated for example by the English national initiative of the Forest Stewardship Council (FSC): "Due to lack of scientific evidence it is not possible at present to give precise guidance on the amount, distribution and composition of dead wood that is appropriate to the individual site" (Anon. 1999). Several national FSC initiatives (e.g. Sweden, Germany, Switzerland) therefore provide only vague qualitative dead wood recommendations, such as "standing dead wood should be created" or "in general, forest owners should maintain some dead trees in a stand". The conclusions of numerous scientific papers emphasising the ecological importance of dead wood only seldom suggest quantitative recommendations (Table 5). Being careful, they remain generally qualitative: "There is a need to increase the input of large dead trees" (Kruys et al. 1999); "It is important to maintain standing dead trees, wherever possible, during harvesting and renewal operations" (Greif and Archibold 2000); "Leave as many large standing dead trees at harvest as possible" (Mccarthy and Bailey 1994).

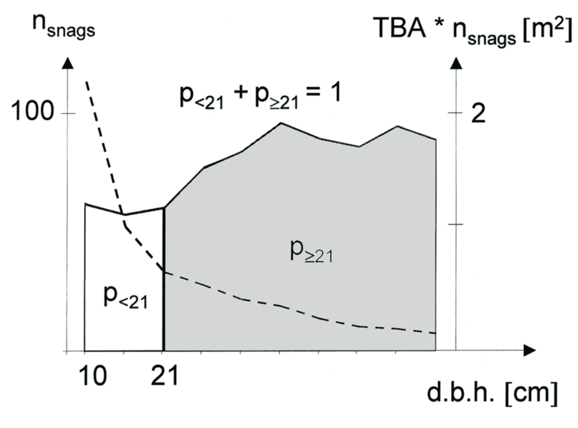

Fig. 4. Experimental determination of the proportion of the total tree basal area for snags with a dbh ≥ 21 cm and < 21 cm, respectively. Number of snags (n_{snags}) – the broken line – on the left axis and tree basal area multiplied with n_{snags} (TBA × n_{snags}) on the right axis. See text for details.

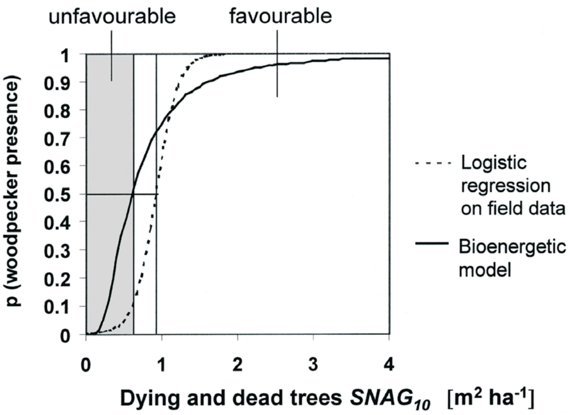

Fig. 5. Comparison of the solution of the bioenergetic model and the regression results of the empirical model. Predicted probability of woodpecker presence as a function of the stand basal area (m^2 ha^{-1}) of dying and dead trees with a dbh ≥ 10 cm.

Quantitative recommendations, however, are essential as operational management goals. Without quantitative targets neither the verification of the progress towards sustainable forest management nor a sound adaptive management is possible. Sippola et al. (1998) argue that quantitative recommendations are too rigid to imitate the variation occurring in natural forests. For example, whereas 5 m^3 ha^{-1} of dead wood may be enough for some species, it would, however, always be too little for other species. The patchy distribution of snags observed in numerous studies argues against the application of uniform targets for snag retention across the landscape (Ganey 1999, Meyer 1999). Thus, in accordance with Sippola et al. (1998) and Ganey (1999), we suggest that a more reasonable goal might be to maintain high snag densities across portions of the landscape, while allowing a smaller than average investment in other areas. Hence quantitative recommendations should be associated with a distribution of the values representing species with different quantitative requirements. In this way the specialised species' requirement regarding the local resource density within the home-range size of a breeding pair could be satisfied even if the recommended mean is considerably lower. Mikusiński et al. (2001) showed that the presence of three-toed woodpeckers was strongly asso-

Table 4. Necessary amounts of standing dying and dead trees required for predicted probabilities of the three-toed woodpecker presence. Comparison between the bioenergetic model results and the results of the logistic regression on field data.

p(woodpecker presence)	Results	$SNAG_{10}$ [•)] [m^2 ha^{-1}]	$SNAG_{10}$ [m^3 ha^{-1}] [*)]	$SNAG_{21}$ [+)] [n ha^{-1}]
0.50	SNAG-model	0.6	7	5.0
	Logistic regr.	0.9	10	
0.75	SNAG-model	1.0	12	8.5
	Logistic regr.	1.0	12	
0.90	SNAG-model	1.6	18	14.0
	Logistic regr.	1.2	14	
0.95	SNAG-model	2.2	25	19.5
	Logistic regr.	1.3	16	

[•)] $SNAG_{10}$: standing dying and dead trees with a dbh ≥ 10 cm.
[*)] approximate volume calculated with (stand basal area × tree height × shape index) according to Lindroth (1995).
[+)] $SNAG_{21}$: standing dying and dead trees with a dbh ≥ 21 cm.

ciated with the presence of other forest bird species. Consequently, in spite of remaining uncertainties and an awareness that quantitative targets will never obtain the full endorsement of the various scientific, political and practical management viewpoints, in this paper we still propose provisional snag target values for the maintenance of biodiversity in spruce forests at the stand scale.

Limitations and further development of the bioenergetic model

The model presented in this paper was based on literature data for bark beetle breeding density, infested tree bark area and woodpecker home-range sizes. Our assumption about the preferred diet of the woodpecker as consisting mainly of bark beetles, i.e. *Ips typographus*, is a simplified view of a real diet that might be much more diverse, especially in the case of endemic bark beetle population levels. Since most studies on woodpecker diets have been conducted during bark beetle outbreak conditions, however, only very little data is currently available on diet components other than bark beetles.

Another point to discuss is the validity of Koplin's (1972) model for the gross energy intake that served as the input for our bioenergetic model. According to Blem (2000), the metabolised energy and the consequent food requirements of birds vary in relation to a complex number of factors, including body size, level of reproductive, digestive and physical activity, phase of moult cycle, radiation, air temperature, wind etc. Koplin's model, considering only air temperature as the most important metabolic factor, is hence a simplified way to calculate energetic requirements. In addition, Koplin developed it for American three-toed woodpeckers and not for European populations. Different energy requirements between woodpecker subspecies cannot be excluded, even if no data is available on this question.

Our model is based on the assumption that three-toed woodpeckers are completely resident in winter and do not leave their breeding home-range during a whole year. While this hypothesis is true for the Alpine subspecies *Picoides tridactylus alpinus* (Glutz von Blotzheim 1994), the nominate subspecies *Picoides tridactylus tridactylus* may undertake a partial migration to winter territories (Hogstad 1970). However, the size of measured winter feeding territories (5.5–8 ha in Hogstad 1970) is so much smaller than breeding home-ranges that the assumption of "all energy sources within the home-range" seems to be acceptable for the nominate subspecies also.

Our model exhibits an asymptotic curve (Figs 2 and 5), suggesting an increase, even if diminishing, of the probability of woodpecker presence with increasing availability of snags. Raphael and White (1984) found that the density of all cavity nesting birds in the Sierra Nevada increased with the density of large snags (> 38 cm dbh) until reaching a snag density of ca 7.5 ha^{-1}. Above this snag density level, bird densities were evidently limited by other factors. Considering these findings, we believe that there is an upper limit of snag density favouring woodpecker presence. Therefore, our model should not be over-interpreted at the upper end. We suggest that it should not be used where the p-value for occurrence is >> 0.95.

Snag targets for the three-toed woodpecker

Our two approaches, undertaken in order to define quantitative snag target values based on three-toed woodpecker habitat preferences, were different. The bioenergetic model was mainly based on theoretical considerations, and its validation performed by a method using remote sensing techniques, i.e. aerial photo interpretation and Geographic Information System (Bütler and Schlaepfer unpubl.). Because of the limitations of these techniques, the results produced involved densities of snags with a minimum dbh of

Table 5. Amounts of dead trees in European sub-Alpine spruce forests a) and recommended quantitative values for standing dead trees in North American and European forests b).

a)	Stand age [yr]	Standing dead trees [m^3 ha^{-1}] Mean (range)	Total lying and standing dead trees [m^3 ha^{-1}] Mean (range)	Authors
Managed forests				
Switzerland		0.0–4.2	3.9–25.8	Guby and Dobbertin (1996)
Switzerland	> 100	12	19	Derleth et al. (2000)
Switzerland	all age classes	9	16	Brassel and Brändli (1999)
Unmanaged forests				
Germany	140–260	28	84 (10–180)	Rauh and Schmitt (1991)
Germany	old		20–60	Utschick (1991)
Poland	all age classes	59	131	Holeksa (2001)
Slovakia	all age classes		80–273	Korpel (1995)
Slovakia	all age classes		42	Korpel (1995)
Slovakia	all age classes		80–220	Korpel (1995)
Switzerland	> 100	32	63	Derleth et al. (2000)

b)	Recommendation	Managed organism	Authors
North America			
California	1 clump per 2 ha of 15 snags > 23 cm dbh	Cavity-nesting birds	Raphael and White (1984)
Oregon	0.35 sound snags > 51 cm dbh ha^{-1}	Pileated woodpecker	Bull and Meslow (1977)
Oregon	≥ 8 snags ha^{-1}	Pileated woodpecker	Bull and Holthausen (1993)
Oregon	≥ 14 snags ha^{-1}	Cavity-nesting birds	Schreiber and Decalesta (1992)
Washington	6 hard and 3 soft snags ha^{-1}	Cavity-nesting birds	Zarnowitz and Manuwal (1985)
Europe			
Germany	≥ 2.5–5 m^3 ha^{-1} (medium term) ≥ 7.5–15 m^3 ha^{-1} (long term)		Ammer (1991)
Germany	5–10 m^3 ha^{-1}, i.e. 1–2% of stems (target value); 20–60 m^3 ha^{-1}, i.e. 5–10% of stems (optimal value)	Birds	Utschick (1991)
Sweden	> 10 snags ha^{-1}	Lesser spotted woodp.	Olsson et al. (1992)
United Kingdom	11–50 snags ha^{-1}, all dbh (medium target); > 50 snags ha^{-1}, all dbh (high target)		Kirby et al. (1998)

21 cm (i.e. numbers of trees ha^{-1}). In contrast, the empirical model started from field measurements executed with the angle relascope technique and resulted in stand basal areas of snags with a minimum dbh of 10 cm (i.e. m^2 ha^{-1}). Due to the different measurement units and a different minimum dbh obtained by each approach, a transformation from n ha^{-1} to m^2 ha^{-1} was necessary for comparison purposes (Fig. 4). In spite of the different approaches, the predicted amounts of required snags were similar at a 70–80% probability of woodpecker presence (Fig. 5, Table 4). This fact allows us to strengthen the reliability of the derived snag targets.

We considered a basal area higher than 0.9 m^2 ha^{-1} (p(woodpecker presence) > 0.5 in both approaches) as favourable for the woodpecker. However, in order to maximise the probability of local woodpecker presence and following the precautionary principle, for management purposes we suggest a higher snag target value. For the last ten years, Swiss three-toed woodpecker populations have been stable or even increasing (Schmid et al. 1998). Among the possible reasons for population growth figures the under-exploitation of marginal mountain forests since the Second World War (Derleth et al. 2000), which is related to a rapid increase in timber harvesting costs (Brassel and Brändli 1999). In such conditions, the amount of dying and dead trees and the available food resources are likely to increase. A possible economic recovery of the timber market, leading to a harvesting intensification of marginal forests, however, could rapidly cause a reversal of the currently positive trend for the woodpecker population. Such considerations emphasise the usefulness of the precautionary principle. Spruce forests favourable to three-toed woodpecker breeding must contain, among other features, sufficient amounts of dying and dead trees. We recommend the following target values for dying and dead trees: ca 1.6 m^2 ha^{-1} (basal area) or 18 m^3 ha^{-1} (volume) of trees with a dbh ≥ 10 cm, corresponding to 14 standing trees per hectare with a dbh of ≥ 21 cm within an area with a size of an average home-range size (44–176 ha); i.e. corresponding to our sampling area of 100 ha. For such levels, the probability of three-toed woodpecker presence in our study was ≥ 0.9. As demonstrated in Fig. 4, large snags are generally rare in managed forests (main mortality of small trees by stem exclusion processes), whereas their contribution to the total basal area is substantial. Considering the prime importance of large snags, we would argue that management recommendations either be given as basal area, or, if expressed in n ha^{-1}, should specify the minimum tree diameter, and the area in ha for which this recommendation applies. Density targets without diameter precision and area of application may fail to fulfil the ecological objective they aimed for (Table 5).

Our targets are higher than the dead wood amounts that have been measured in managed Swiss sub-Alpine forests, while they do not reach amounts measured in unmanaged forests (Table 5). Considering mean values for living trees in Swiss forests of 32.3 m^2 ha^{-1} and 354 m^3 ha^{-1} (Brassel and Brändli 1999), the suggested snag target values represent not more than 5% of the living wood stock. We argue that, even in production forests, such a loss in favour of biodiversity should be acceptable.

Our values are of the same order of magnitude as the snag retention recommendations for North American and European forests that are based on cavity-nesting birds or other woodpecker species (Table 5). They are higher than Ammer's (1991) recommendations, which were not, however, based on ecological preferences of birds. Many snag requirements for different woodpecker species are based only on their use of snags as nesting trees (Imbeau and Desrochers 2002). They implicitly assume that snags required for nesting are an important limiting factor to woodpecker populations. Imbeau and Desrochers (2002) argued that such models are highly unlikely to be successful in predicting long-term habitat needs, considering the extensive use of snags for foraging. Unlike these models, our snag retention prescriptions are designed to ensure a continuous supply of foraging trees and go beyond the aim of maintaining a supply of potential nesting trees.

So far quantitative recommendations for forest management have been made mainly for the scales of trees and stands, but rarely for forest management units and landscapes. However, maintenance of viable populations involves the provision of targets at multiple spatial and temporal scales (Larsson 2001, Angelstam et al. 2004). Using area-demanding birds as modelling tools stresses the need for formulating targets at the levels of individuals, populations as well as metapopulations. For Alpine and boreal forests, bird groups such as woodpeckers (e.g., Pechacek and d'Oleire-Oltmanns in press), grouse (e.g., Angelstam et al. 2001) and resident tits (e.g., Jansson and Angelstam 1999) are important focal species to begin with.

Hence, for a species as the three-toed woodpecker, which is dependent on a continuous supply in space and time of snags of a particular quality, there still remains work to be able to formulate targets within the framework of sustainable forestry for the following issues: 1) How far apart can home-range sized areas exceeding the stand scale target be? 2) What proportion of a landscape needs to be in what phase of successional development of snags to maintain a local viable population? 3) Finally, in regions with other forest dynamics than the gap-phase dominated one prevailing in Alpine forests, the large-scale succession after stand-replacing disturbances need to be accounted for.

Conclusion

In this study we presented a model based on energetic needs of three-toed woodpeckers. Although simple, it enabled the quantification of snag requirements for this woodpecker species, which has been corroborated by a field study approach. The results made it possible to identify the snag quantities of local forest patches that are necessary to maximise the probability of local three-toed woodpecker presence. Forest patches presenting optimal quantities may be mapped and integrated into management planning concepts in order to define strategies for the maintenance of local populations of this bird species. Since the three-toed woodpecker is an indicator of forest biodiversity, management aimed at the maintenance of this species will also enable the fulfilment of other biodiversity goals.

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