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Post-harvest seedling recruitment following mountain pine beetle infestation of Colorado lodgepole pine stands: a comparison using historic survey records

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Abstract: The extent and severity of overstory lodgepole pine (*Pinus contorta* var. *latifolia* Engelm. ex Wats.) mortality from mountain pine beetle (*Dendroctonus ponderosae* Hopkins) has created management concerns associated with forest regeneration, wildfire risk, human safety, and scenic, wildlife, and watershed resources in western North America. Owing to the unprecedented nature of the outbreak and associated management in the southern Rocky Mountains, it is unknown if the forests that regenerate after this current period of extensive change will differ from those that regenerated in the past. Here, we compare the density and species composition of post-harvest seedling recruits in pre-outbreak (1980–1996) and outbreak stands (2002–2007). Lodgepole pine accounted for more than 95% of post-harvest seedling recruitment and the density of seedlings colonizing clearcuts was equal during both the pre-outbreak and outbreak periods. Compared with harvested areas, the density of tree regeneration was 75% lower in uncut forests and was more evenly distributed among subalpine fir (*Abies lasiocarpa* (Hook.) Nutt.) and lodgepole pine. This comparison provides evidence that the density of seedling recruitment will be at least as high after extensive pine beetle caused mortality as under healthy, pre-outbreak conditions and that the species composition of stands regenerating after this outbreak will differ between treated and untreated areas.

Résumé : L'étendue et la sévérité de la mortalité des tiges dominantes de pin tordu latifolié (*Pinus contorta* var. *latifolia* Engelm. ex Wats.) causée par le dendroctone du pin ponderosa (*Dendroctonus ponderosae* Hopkins) a engendré des problèmes d'aménagement associés à la régénération forestière, au risque de feux de forêt, à la sécurité humaine ainsi qu'aux ressources visuelle, faunique et hydrique dans l'ouest de l'Amérique du Nord. À cause du caractère inédit de l'épidémie et de l'aménagement qui en découle dans la partie méridionale des Montagnes Rocheuses, nous ne savons pas si les forêts qui se régénèrent après cette période de changements intensifs seront différentes de celles qui se sont régénérées dans le passé. La présente étude compare la densité et la composition en espèces des semis recrutés après la coupe en périodes pré-épidémique (1980–1996) et épidémique (2002–2007). Plus de 95 % des semis recrutés après la coupe sont des semis de pin tordu latifolié et la densité des semis qui ont colonisé les coupes à blanc en période pré-épidémique est la même qu'en période épidémique. Comparativement aux aires récoltées, la densité de la régénération arborescente est 75 % plus faible dans les forêts non coupées et plus équitablement distribuée entre le sapin subalpin (*Abies lasiocarpa* (Hook.) Nutt.) et le pin tordu latifolié. Cette comparaison fournit la preuve que la densité des semis recrutés sera au moins aussi forte après une mortalité sévère causée par le dendroctone du pin ponderosa qu'elle l'était dans les peuplements sains en période pré-épidémique et que la composition en espèces des peuplements qui se seront régénérés après cette épidémie sera différente dans les aires coupées et non coupées.

[Traduit par la Rédaction]

Introduction

In Colorado, nearly 1.2 million hectares (3 million acres) of pine forest have been infested by mountain pine beetle (*Dendroctonus ponderosae* Hopkins) since 1996 (Colorado State Forest Service 2008; USDA Forest Service 2009). Bark beetles killed 10.5 million lodgepole pine (*Pinus contorta* var. *latifolia* Engelm. ex Wats.) trees in Colorado be-

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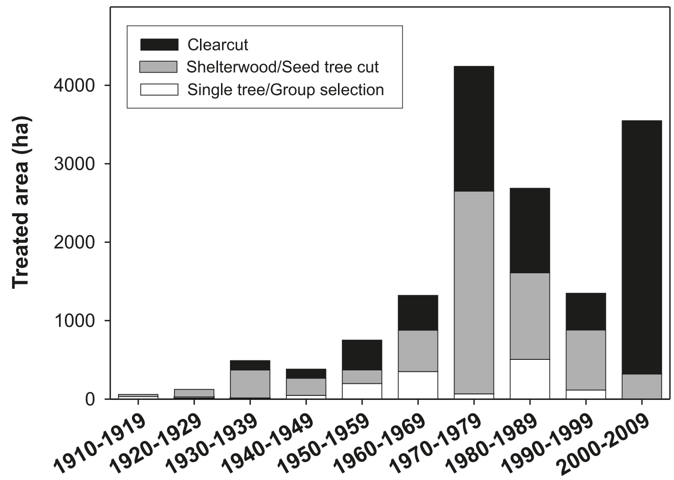
tween 2002 and 2007, a 10-fold increase in mortality over the previous 5-year period (Thompson 2009). In infested stands, live lodgepole basal area is typically reduced by 70% and may exceed 90% in mature, even-aged stands (Klutsch et al. 2009; Sulphur Ranger District, unpublished data). Increased annual mean and winter minimum temperatures, prolonged drought, and aging forest stands have been implicated in the current decline in the health of western forests (Amman 1982; Jenkins et al. 2008). The geographic extent and severity of overstory mortality caused by recent mountain pine beetle outbreaks provides an example of how climate change may impact North American forests (Logan et al. 2003; Raffa et al. 2008; van Mantgem et al. 2009).

Lodgepole pine is a disturbance-adapted species that typically regenerates rapidly into even-aged stands after wildfire or forest harvest (Lotan and Perry 1983). However, lodgepole pine establishment can be inhibited where availability of viable seed is low or where canopy mortality or harvesting is not accompanied by forest floor disturbance and exposure of a mineral seedbed. Mechanical scarification often accompanies lodgepole pine harvest operations to reduce herbaceous competition and create adequate seedbed cover (Lotan 1964; Landhäusser 2009). Limited exposure of seedbed and competition from moss contributed to tree regeneration failure following bark beetle infestation in British Colombia lodgepole pine forests (Astrup et al. 2008). In contrast, in untreated beetle-killed lodgepole pine forests in Colorado, a cohort of pine seedlings established 3–5 years after bark beetle infestation (Collins 2010).

Pine beetle activity reached epidemic levels during the late 1990s in northern Colorado and has led to a rapid and dramatic increase in forest harvesting (USDA Forest Service 2005; Colorado State Forest Service 2008). On the Sulphur Ranger District (Arapaho-Roosevelt National Forest) at the center of the current outbreak area, lodgepole pine forests susceptible to mountain pine beetle infestation comprise nearly half the total area and the majority of the forested area in the district (USDA Forest Service 2008, 2009). Since the early 1980s, growing human populations in mountain communities, decreased public support for active forest management, increased production costs, and harvesting restrictions caused a decline in the forest industry and timber harvesting on US Forest Service land in Colorado (Fig. 1) and elsewhere (Longwell and Lynch 1990; Cubbage et al. 1995). The current level of mountain pine beetle caused mortality has generated renewed public support for forest management. Since the year 2000, there have been 3700 ha of lodgepole pine dominated forests salvage logged to reduce fuel loads and regenerate new stands. This represents a 2.5-fold increase in harvesting over the previous decade. Clearcut harvests cover 90% of the treated area, and the area clear-cut since the year 2000 surpasses the extent of area clear-cut during any decade in the past (Fig. 1).

Owing to its unprecedented scope and rapid onset, it remains unknown if the forests that regenerate following the current outbreak and associated management will differ from those that regenerated in the past. Our objective was to provide initial information about post-outbreak forests in Colorado by comparing seedling recruitment in similar stands that were salvage logged following the beetle outbreak and stands cut in the past under healthier forest conditions. We also compared seedling recruitment densities in harvested areas with advance regeneration densities in uncut stands. For this assessment, we utilized stand inventory and post-harvest seedling recruitment records from the first stands harvested in Colorado in response to the current beetle infestation.

Fig. 1. Commercial harvesting activities within the Sulphur Ranger District, Arapaho-Roosevelt National Forest, Colorado. Records exist since establishment of the Arapaho National Forest in 1908.



Methods

Study area and stand selection

This study was conducted in the Williams Fork Drainage of the Arapaho-Roosevelt National Forest in the Colorado Front Range approximately 100 km west of Denver. Local climate is temperate and continental with long, cold winters and short, cool summers. Mean annual air temperature is 0.6 °C with January and July average temperatures of –10 and 12.2 °C, respectively (Fraser Experimental Forest, unpublished data). Total annual precipitation averages 600 mm; snowfall received between October and May comprises 64% of total annual precipitation and summer rains contribute the balance. Lodgepole pine stands dominate the lower elevations (i.e., 2750–3050 m) and south-aspect slopes (Huckaby and Moir 1998). Mixed-species forests of subalpine fir (*Abies lasiocarpa* (Hook.) Nutt.), Engelmann spruce (*Picea engelmannii* Parry ex Engelm.), and lodgepole pine occupy valley bottom and north-facing slopes and extend to treeline (3300–3500 m). Quaking aspen (*Populus tremuloides* Michx.) occurs in small clonal stands scattered throughout the lower elevations.

Stand inventory and post-harvest seedling recruitment data from pre-outbreak (1980–1996, n = 32) and outbreak (2002–2007, n = 30) periods were gathered by the Sulphur Ranger District, Arapaho-Roosevelt National Forest. Pre-outbreak stands were harvested during a period of endemic mountain pine beetle activity. During the outbreak period, bark beetles reduced live basal area to below 11.5 $m^2 \cdot ha^{-1}$ in stands selected for harvest. All harvest areas were clear-cut units in lodgepole pine dominated stands (i.e., 71%–100% of basal area) (Table 1). Overstory stand density and quadratic mean diameter were comparable between the two

Table 1. Overstory and advance regeneration conditions in uncut pre-outbreak (n = 32) and outbreak stands (n = 30) on the Sulphur Ranger District, Arapaho-Roosevelt National Forest.

	Overstory			
	Quadratic mean diameter (cm)	Basal area ($m^2 \cdot ha^{-1}$)	Density ($trees \cdot ha^{-1}$)	Advance regeneration: density ($trees \cdot ha^{-1}$)
Pre-outbreak (1980–1996)				
Lodgepole pine	18.0	36.1	1578	554
Subalpine fir	9.9	1.2	308	257
Engelmann spruce	24.8	0.7	78	59
Outbreak (2002–2007)				
Lodgepole pine	17.3	25.6	1475	895
Subalpine fir	6.5	0.9	821	768
Engelmann spruce	15.9	0.5	46	37

Note: Overstory data includes live and dead trees. Overstory trees were surveyed in variable-radius plots. Advance regeneration (≤140 cm tall) was sampled in 3.6 m fixed-radius plots at a density of 0.5 $plot \cdot ha^{-1}$.

time periods. Clearcut treatments typically retain <9.2 and 4.6 $m^2 \cdot ha^{-1}$ of live and dead basal area, respectively, in this region. Pre-outbreak and outbreak stands were intermixed within a 100 km^2 portion of the Williams Fork drainage.

Sampling and statistical analysis

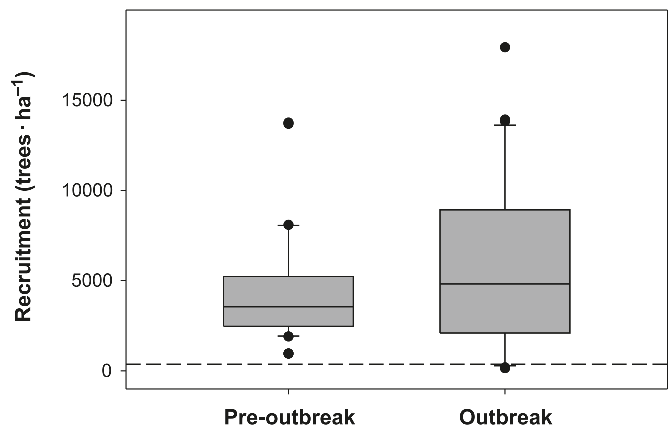
We compared the density and species composition of advance regeneration (≤140 cm tall) in uncut stands prior to harvest and seedlings (<15 cm tall) in clearcut units surveyed 3 years after harvesting. In uncut and harvested areas, sample plots (3.6 m radius) were randomly located at a density of one plot per 2 ha. Seedling recruitment was spatially clumped with seedlings absent from approximately one quarter of sample plots and >400 recruits in other plots. To account for the nonnormal and overdispersed distribution of the data, we compared population means using the nonparametric multiresponse permutation procedure. The multiresponse permutation procedure assumes the exchangeability of observational units and does not depend on normality or homogeneity of variance (Cai 2006). Overstory trees in uncut stands were surveyed using variable-radius prism plots.

We also tested the significance of site characteristics as predictors of recruitment. Site characteristics (canopy condition at time of harvest, pre-harvest overstory species composition and basal area, elevation, and aspect) were tested as predictors of post-harvest recruitment and advance regeneration density using a backwards elimination regression approach (Neter et al. 1989; Whittingham et al. 2006). To account for overdispersion, we applied a negative binomial distribution. Goodness of fit was assessed with Pearson's χ^2 statistic (White and Bennetts 1996; SAS Institute Inc. 2008).

Results and discussion

Lodgepole pine accounted for 96% and 97% of post-harvest seedling recruitment during the pre-outbreak and outbreak periods, respectively. The density of third-year post-harvest seedling recruits did not differ statistically between pre-outbreak and outbreak periods (4430 versus 5736 $recruits \cdot ha^{-1}$; multiresponse permutation procedure, p = 0.12) (Fig. 2). Subalpine fir contributed the balance of post-harvest seedling recruitment. Lodgepole pine density was highly variable in the post-harvest seedling records that we surveyed; average stand densities ranged from 950 to 14 000 and from 150 to 18 000 $seedlings \cdot ha^{-1}$ in the pre-outbreak and outbreak periods, respectively (Fig. 2). Seedling densities were more variable in outbreak post-harvest surveys.

Fig. 2. Post-harvest recruitment in pre-outbreak (n = 32) and outbreak stands (n = 30) 3 years after harvest. Lodgepole pine accounts for 97% of all recruits. Boxes show the median and 25th and 75th percentiles, whiskers represent the 10th and 90th percentiles, and circles represent observations outside the 10th and 90th percentiles. The broken line shows the minimum density (370 $trees \cdot ha^{-1}$) of undamaged seedlings required to certify successful stocking (USDA Forest Service 1997).



In general, post-harvest seedling recruitment was high (~4700 $recruits \cdot ha^{-1}$) during both pre-outbreak and outbreak periods, and few plots failed to restock with new seedlings. In lodgepole pine forests of the southern Rockies, a minimum of 370 $trees \cdot ha^{-1}$ are required on 70% of plots to certify that treated areas have regenerated successfully (USDA Forest Service 1997). Managers in the region consider that development of well-stocked stands require post-harvest seedling densities about 10-fold above the minimum threshold (i.e., ≥3000 $stems \cdot ha^{-1}$). In our study, post-harvest recruitment surpassed minimum stocking requirements in 100% and 94% of pre-outbreak and outbreak harvest units, respectively. More than half of the harvest units (68% and 57% in pre-outbreak and outbreak units, respectively) had sufficient new recruits to support formation of well-stocked forests.

Seedling density failed to meet minimum stocking thresholds in only 3 of 62 total units. Two of the poorly stocked units were among the highest elevation in the study area (~3100 m). Overall, lodgepole recruitment declined significantly with increasing elevation in both pre-outbreak (β = –5.18, p = 0.06) and outbreak harvest units (β = –5.35, p = 0.08). The third poorly stocked unit occurred at 2600 m in a lower landscape position where competition with graminoid vegetation (e.g., *Calamagrostis rubescens* Buckl. and *Carex geyeri* Boott) commonly inhibits lodgepole recruitment (Lotan 1975).

Clearing size often determines the amount of seed available to regenerate lodgepole pine harvest areas (Lotan and Perry 1983; Alexander 1986). Mean clearing size was fourfold greater during the outbreak (17 ha average, 2–55 ha range) compared with the pre-outbreak periods (4 ha average, 0.5–14 ha range). Pre-outbreak treatments targeted small pockets of lodgepole pine and were designed to provide adequate seed dispersal from adjacent uncut stands (Alexander 1986; Lessard et al. 1987). During beetle salvage operations, harvest size was determined primarily by the road network, terrain, and access to beetle-killed pine. There was, however, no relationship between clearing size and seedling recruitment in either era (p = 0.40). We have observed that crowns of beetle-killed pine trees typically shatter when felled and disperse cones more broadly than during green tree harvesting, providing adequate cone and seed dispersal to support dense pine regeneration.

In the untreated stands that will dominate the post-outbreak landscape, the density and composition of advance regeneration will be critical to forest regeneration. Although the current outbreak has affected nearly 1.2 million ha in Colorado, the vast majority of federal lands will remain untreated. For example, owing to terrain, staffing, and economic constraints, beetle salvage activities will not exceed 15% of the potentially treatable area on the Sulphur Ranger District. The density of advance regeneration in uncut forests was 75% lower than the density of seedling recruitment in harvested areas (1285 versus 4700 trees·ha^{-1}), but the total density of advance regeneration did not differ between harvest eras (p = 0.21). We found that the density of lodgepole advance regeneration declined with increased overstory basal area in both pre-outbreak (β = –0.012, p = 0.01) and outbreak stands (β = –0.021, p = 0.03). Compared with harvested areas, advance regeneration in untreated stands is more evenly distributed among subalpine fir and lodgepole pine, with lodgepole comprising 64% and 53% of advance regeneration in the pre-outbreak and outbreak periods, respectively (Table 1). Similarly, in uncut beetle-killed stands at the Fraser Experimental Forest, the density of subalpine fir advanced regeneration was 2.3-fold greater than lodgepole regeneration (Collins 2010).

This comparison of historic US Forest Service records provides evidence that the density of seedling recruitment will be at least as high after extensive mountain pine beetle caused mortality as before the outbreak and that the future species composition may differ between treated and untreated stands. Our study area includes some of the earliest results of the management response to the current mountain pine beetle outbreak. This comparison offers an initial estimate of forest recovery following unprecedented overstory mortality in harvested and uncut lodgepole pine stands in Colorado and may have broader implications for western North America. The use of preexisting US Forest Service survey records allowed us to provide a rapid, low-cost initial estimate of the tree density and composition of forests developing in areas harvested in response to unprecedented beetle outbreak in the southern Rockies.

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References

Alexander, R.R. 1986. Silvicultural systems and cutting methods for old-growth lodgepole pine forests in the central Rocky Mountains. Gen. Tech. Rep. 127. Rocky Mountain Forest and Range Experiment Station, Fort Collins, Co.

Amman, G.D. 1982. The mountain pine beetle–identification, biology, causes of outbreaks and entomological research needs. Inf. Rep. BC-X 230. Canadian Forestry Service, Pacific Forest Research Centre, Victoria, B.C. pp. 7–12.

Astrup, R., Coates, K.D., and Hall, E. 2008. Recruitment limitations in forests: Lessons from an unprecedented mountain pine beetle epidemic. For. Ecol. Manag. **256**(10): 1743–1750. doi:10.1016/j.foreco.2008.07.025.

Cai, L. 2006. Multi-response permutation procedure as an alternative to the analysis of variance: an SPSS implementation. Behav. Res. Methods, **38**(1): 51–59. PMID:16817513.

Collins, B.J. 2010. Initial and future stand development following mountain pine beetle in harvested and uncut lodgepole pine forests. M.Sc. thesis, Department of Forest, Rangeland, and Watershed Stewardship, Colorado State University, Fort Collins, Co.

Colorado State Forest Service. 2008. The health of Colorado's forests 2008 report. Available from csfs.colostate.edu/pages/pub-csfs2.html [accessed 2 December 2009].

Cubbage, F.W., Harris, T.G., Wear, D.N., Abt, R.C., and Pacheco, G. 1995. Timber supply in the south: where is all the wood? J. For. **93**(7): 16–20.

Huckaby, L.S., and Moir, W.H. 1998. Forest communities at Fraser Experimental Forest, Colorado. Southwest. Nat. **43**(2): 204–218.

Jenkins, M.J., Herbertson, E., Page, W., and Jorgensen, C.A. 2008. Bark beetles, fuels, fires and implications for forest management in the Intermountain West. For. Ecol. Manag. **254**(1): 16–34. doi:10.1016/j.foreco.2007.09.045.

Klutsch, J.G., Negron, J.F., Costello, S.L., Rhoades, C.C., West, D.R., Popp, J., and Caissie, R. 2009. Stand characteristics and downed woody debris accumulations associated with a mountain pine beetle (*Dendroctonus ponderosae* Hopkins) outbreak in Colorado. For. Ecol. Manag. **258**(5): 641–649. doi:10.1016/j.foreco.2009.04.034.

Landhäusser, S.M. 2009. Impact of slash removal, drag scarification, and mounding on lodgepole pine cone distribution and seedling regeneration after cut-to-length harvesting on high elevation sites. For. Ecol. Manag. **258**(1): 43–49. doi:10.1016/j.foreco.2009.03.045.

Lessard, G., Hildebrand, D., and Haneman, D.E. 1987. Forest pest conditions in the Rocky Mountain Region 1986. Available from

USDA Forest Service, Rocky Mountain Region, Timber, Forest Pest and Cooperative Forest Management, Lakewood, Co.

Logan, J.A., Regniere, J., and Powell, J.A. 2003. Assessing the impacts of global warming on forest pest dynamics. Front. Ecol. Environ. **1**(3): 130–137. doi:10.1890/1540-9295(2003)001[0130:ATIOGW]2.0.CO;2.

Longwell, R.T., and Lynch, D.L. 1990. Colorado logging accidents: 1984–1988. Is it safe in the woods? West. J. Appl. For. **5**(4): 132–135.

Lotan, J.E. 1964. Regeneration of lodgepole pine: a study of slash disposal and cone opening. U.S. For. Serv. Res. Note INT-16.

Lotan, J.E. 1975. Regeneration of lodgepole pine forests in the northern Rocky Mountains. *In* Management of lodgepole pine ecosystems: Symposium Proceedings, 9–11 October 1973, Pullman, Washington. *Edited by* D. Baumgartiner. Washington State University Extension Service, Pullman, Wash. pp. 516–535.

Lotan, J.E., and Perry, D.A. 1983. Ecology and regeneration of lodgepole pine. U.S. Dep. Agric. Agric. Handb. No. 606.

Neter, J., Wasserman, W., and Kutner, M.H. 1989. Applied linear regression models. 2nd ed. Homewood, Irwin, Ill.

Raffa, K.F., Aukema, B.H., Bentz, B.J., Carroll, A.L., Hicke, J.A., Turner, M.G., and Romme, W.H. 2008. Cross-scale drivers of natural disturbances prone to anthropogenic amplification: the dynamics of bark beetle eruptions. Bioscience, **58**(6): 501–517. doi:10.1641/B580607.

SAS Institute Inc. 2008. SAS version 9.2. SAS Institute Inc., Cary, N.C.

Thompson, M.T. 2009. Analysis of conifer mortality in Colorado using Forest Inventory and Analysis's Annual Forest Inventory. West. J. Appl. For. **24**(4): 193–197.

USDA Forest Service. 1997. 1997 revision of the land resource management plan. Arapaho and Roosevelt National Forests and Pawnee National Grassland, Fort Collins, Colo. Available from www.fs.fed.us/r2/arnf/projects/forest-planning/management-plan/index.shtml [accessed 18 September 2009].

USDA Forest Service. 2005. Environmental assessment, Upper Fraser Valley forest health project. Sulphur Ranger District, Arapaho and Roosevelt National Forests and Pawnee National Grassland, Grand County, Co.

USDA Forest Service. 2008. 2008 Sulphur Ranger District project summary. Arapaho and Roosevelt National Forests and Pawnee National Grassland, Fort Collins, Colo. Available from www.fs.fed.us/r2/arnf/conditions/srdbarkbeetle/addressingbeetle.shtml [accessed 10 December 2009].

USDA Forest Service. 2009. Forest insect and disease aerial survey data, Rocky Mountain region. Available from www.fs.fed.us/r2/resources/fhm/aerialsurvey/download/ [accessed 15 December 2009].

van Mantgem, P.J., Stephenson, N.L., Byrne, J.C., Daniels, L.D., Franklin, J.F., Fulé, P.Z., Harmon, M.E., Larson, A.J., Smith, J.M., Taylor, A.H., and Veblen, T.T. 2009. Widespread increase of tree mortality rates in the western United States. Science, **323**(5913): 521–524. doi:10.1126/science.1165000. PMID:19164752.

White, G.C., and Bennetts, R. 1996. Analysis of frequency count data using the negative binomial distribution. Ecology, **77**(8): 2549–2557. doi:10.2307/2265753.

Whittingham, M.J., Stephens, P.A., Bradbury, R.B., and Freckleton, R.P. 2006. Why do we still use stepwise modelling in ecology and behaviour? J. Anim. Ecol. **75**(5): 1182–1189. doi:10.1111/j.1365-2656.2006.01141.x. PMID:16922854.