



# THÈSE

En vue de l'obtention du

## DOCTORAT DE L'UNIVERSITÉ DE TOULOUSE

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Université Toulouse 3 Paul Sabatier (UT3 Paul Sabatier)

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**Titre :**

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propositions de gestion conservatoire

- Annexes -

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# **Annexes**

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# Annexe 1 : Représentations du domaine vital des individus (Chapitre 6) : Représentations du domaine vital des individus, via l'utilisation du Kernel 95% avec $h_{ref}$ , $h_{LSCV}$ et $h_{CV}$ , puis du polygone incrémenté par grappes (ICP).

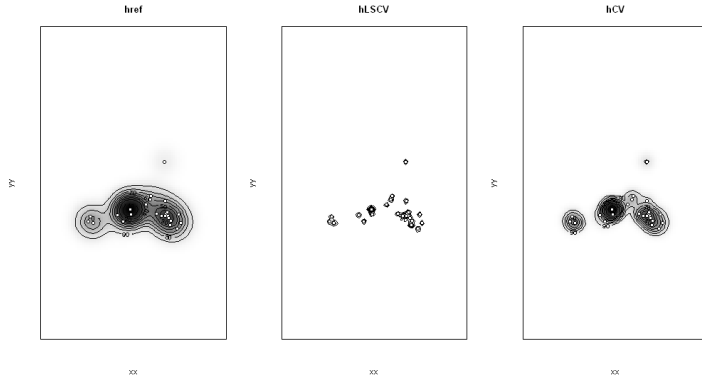
Les figures ci-dessous représentent la forme du domaine vital DV obtenu à l'aide de R pour chaque individu, à partir de la méthode du kernel (pour les 3 méthodes disponibles :  $h_{ref}$ ,  $h_{LSCV}$ , et  $h_{CV}$ ). A chaque représentation a été associée une valeur de l'AICc calculée à l'aide du logiciel Animal Space Use, permettant de retenir la représentation la plus fiable des trois. Le modèle retenu est noté dans la colonne de droite, au-dessus de la représentation du DV obtenu par la méthode du polygone incrémenté par grappes ICP. L'ICP est à préférer au MCP pour les DV multinucléaires ou binucléaires, et inversement pour les DV uninucléaires. Le choix entre les 2 représentations (ICP ou MCP) est donc noté à côté du modèle de représentation par le kernel retenu. Type de modèle obtenu à partir des valeurs d'AICc : CU : unimodal ; BVN : bimodal ; 2CN et 2BVN : multimodal.

## *Myotis bechsteinii*

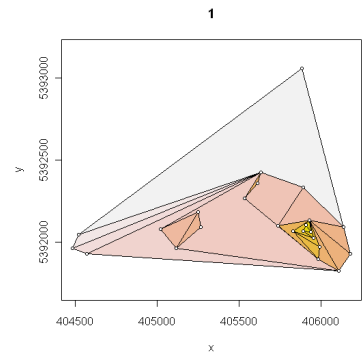
### Site : Forêt Domaniale de Rambouillet

Kernel avec $h_{ref}$	Kernel avec $h_{LSCV}$	Kernel avec $h_{CV}$	ICP
1Mbe2006-1-M-A-478 (locs : 105)			$h_{CV}$ (2CN), DV multimodal : ICP
1Mbe2006-2-F-A-558 (locs : 20)			$h_{ref}$ (2BVN), DV multimodal : ICP
1Mbe2006-2-F-A-578 (locs : 42)			$h_{CV}$ (2CN), DV multimodal : ICP

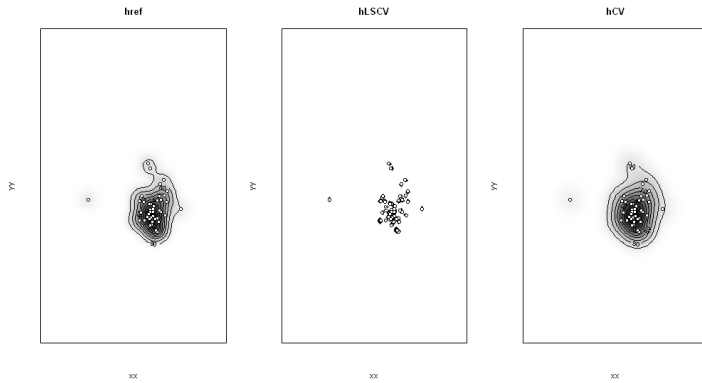
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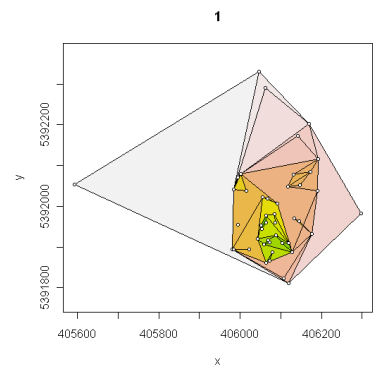
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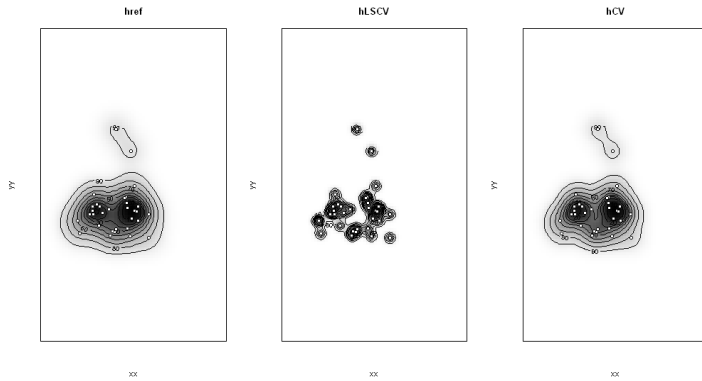
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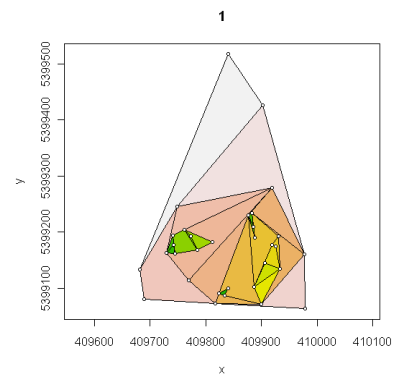
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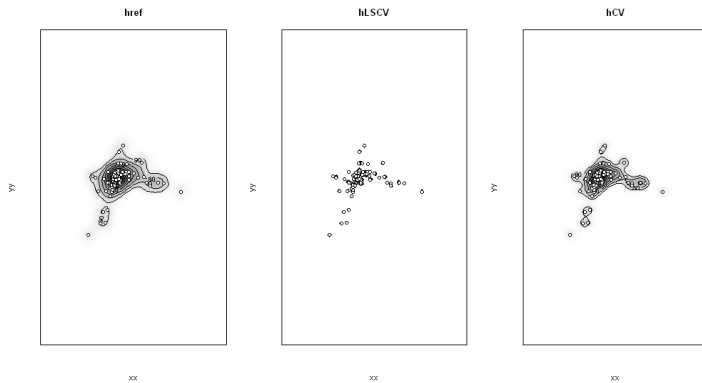
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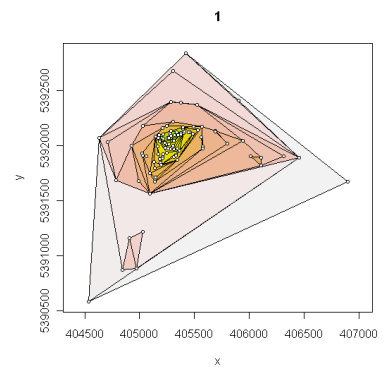
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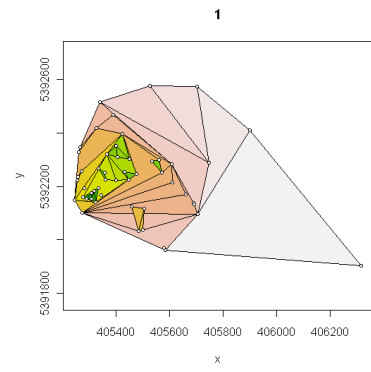
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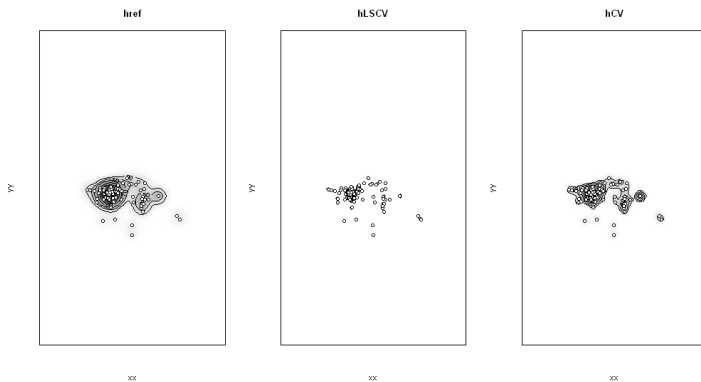
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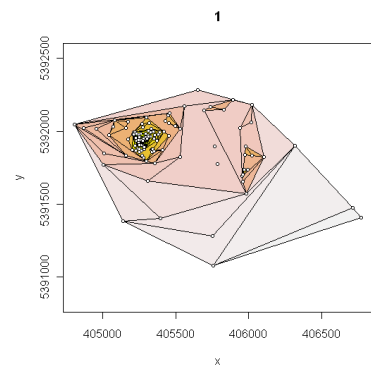
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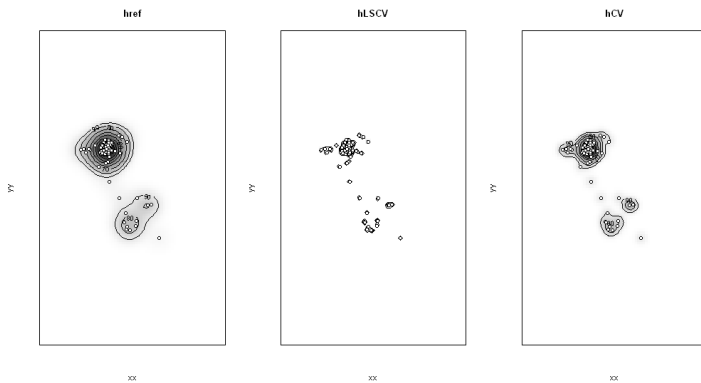
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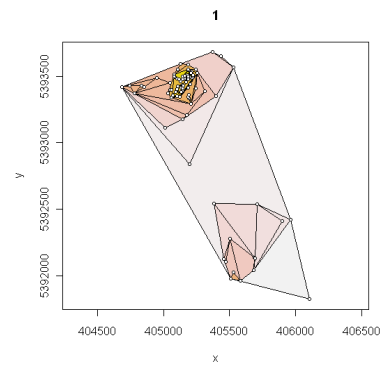
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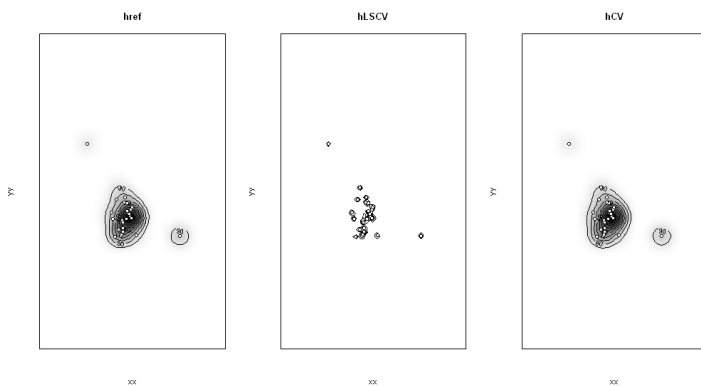
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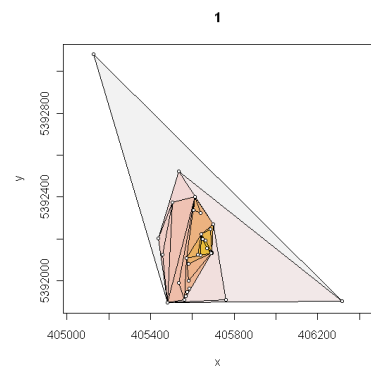
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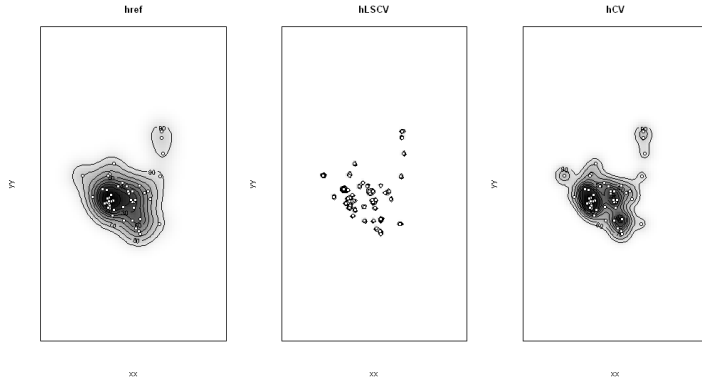
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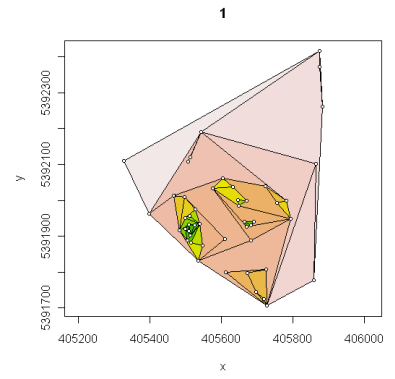
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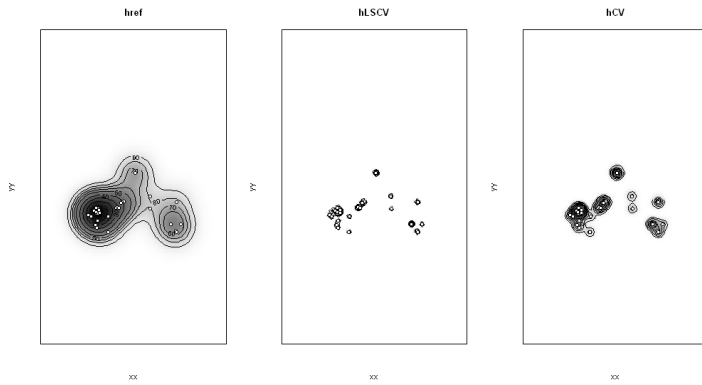
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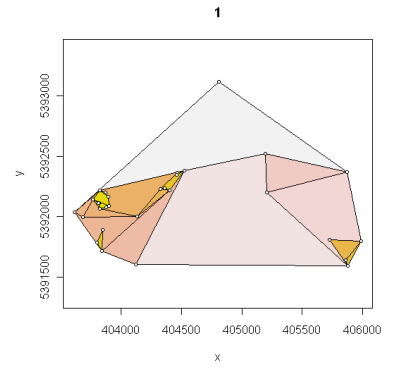
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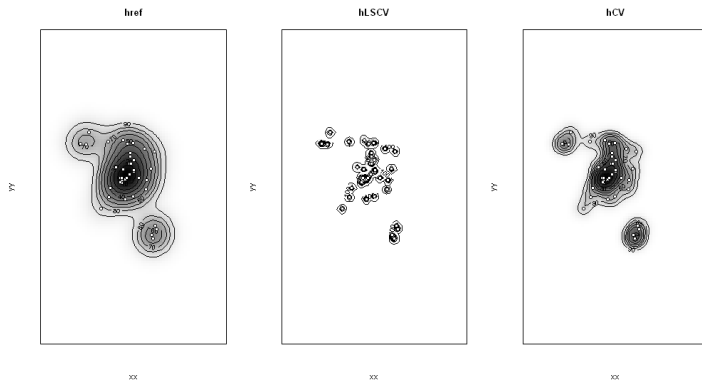
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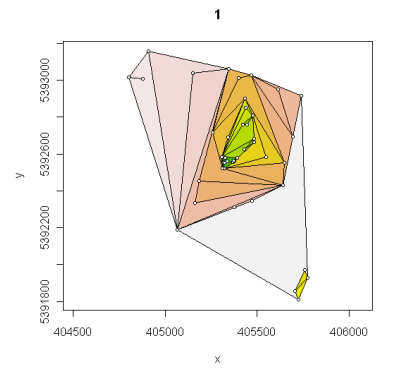
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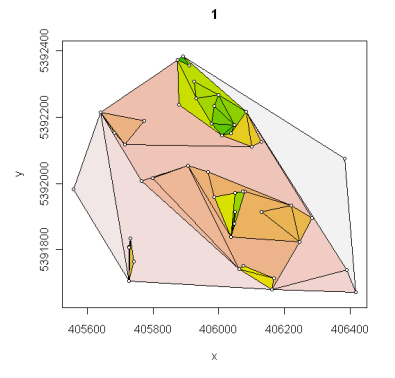
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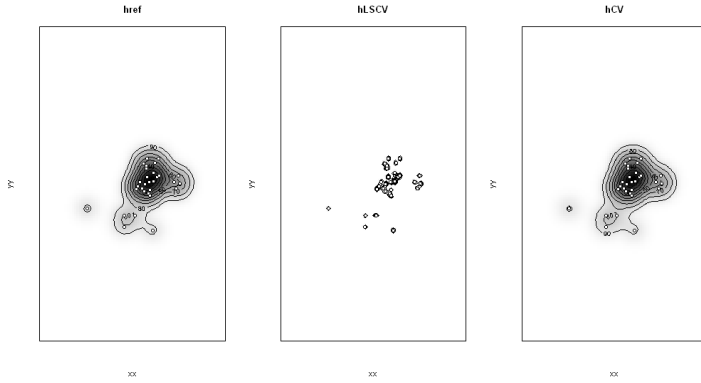
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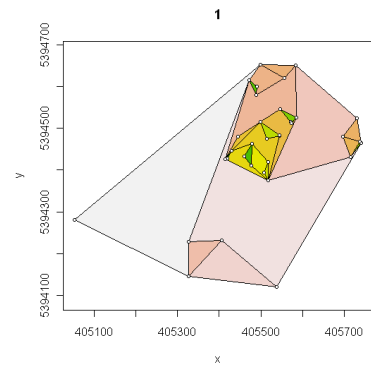
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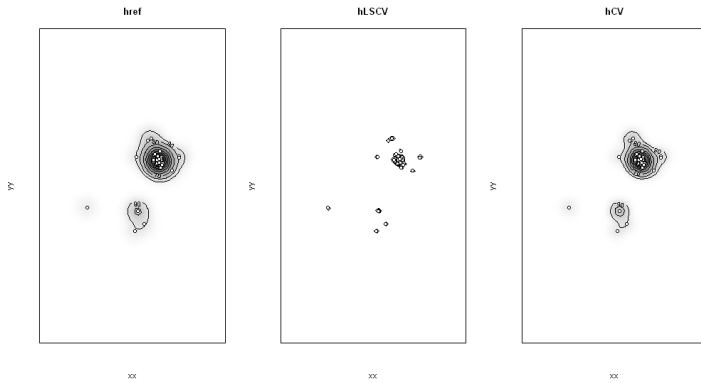
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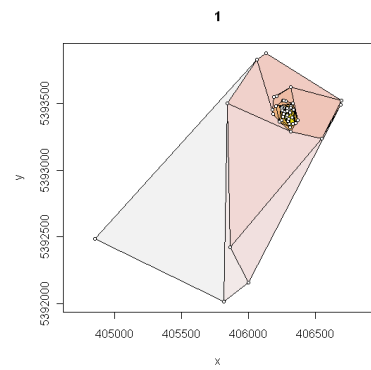
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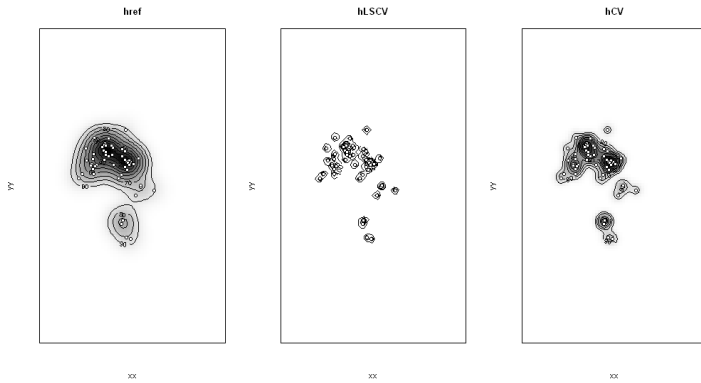
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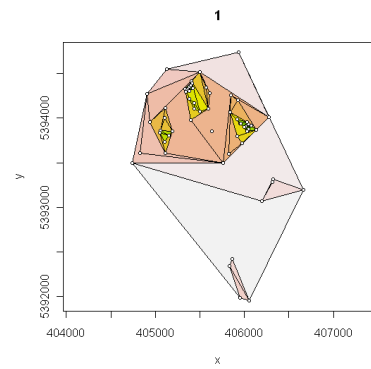
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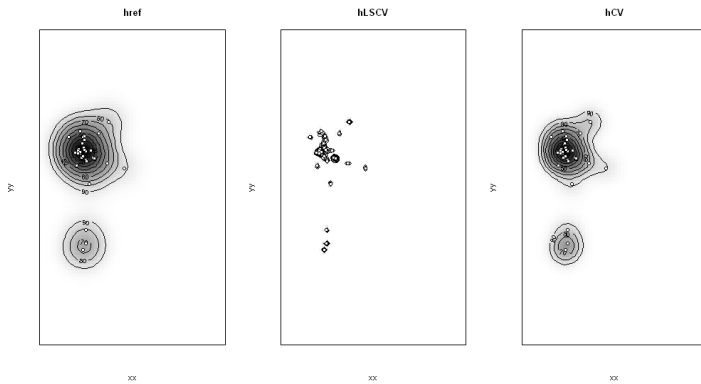
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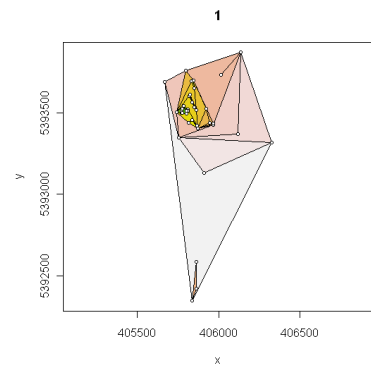
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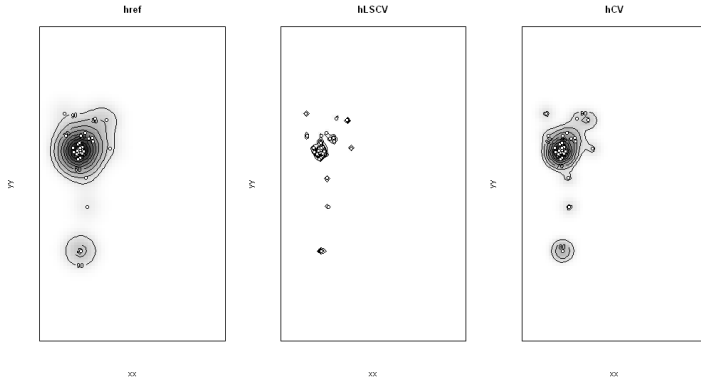


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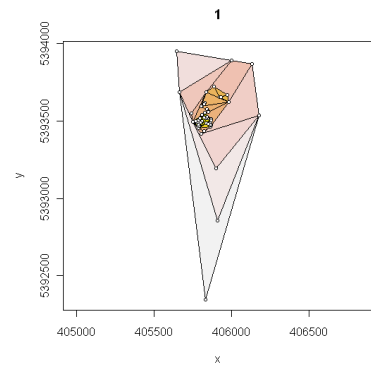




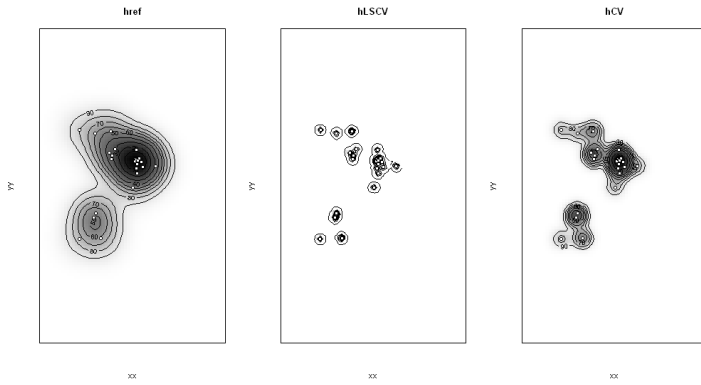
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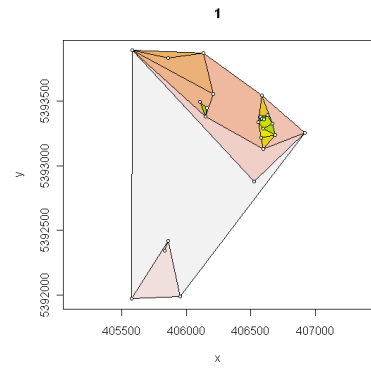
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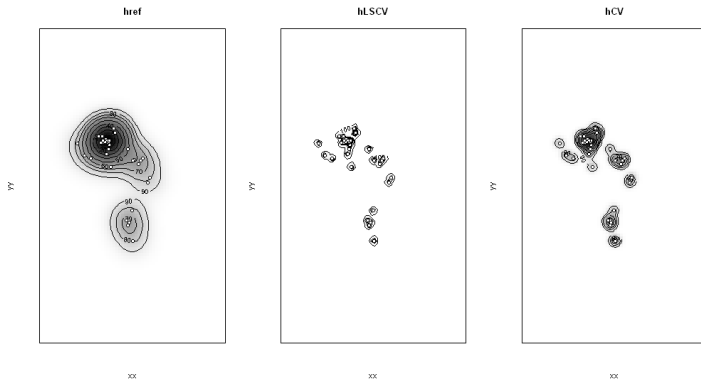
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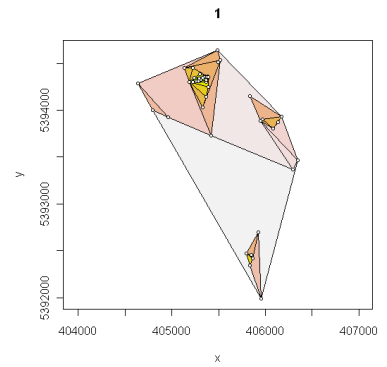
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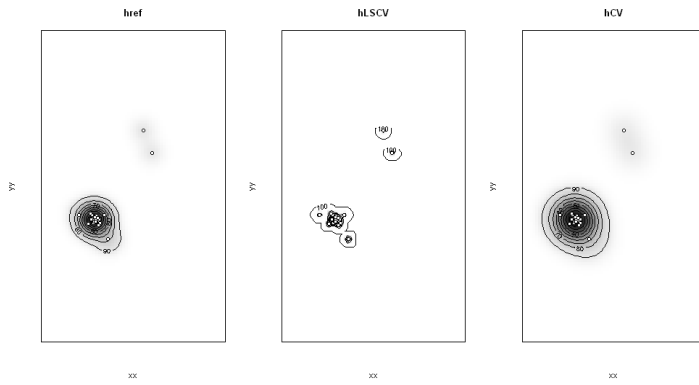
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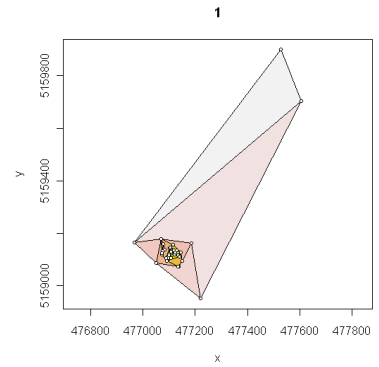
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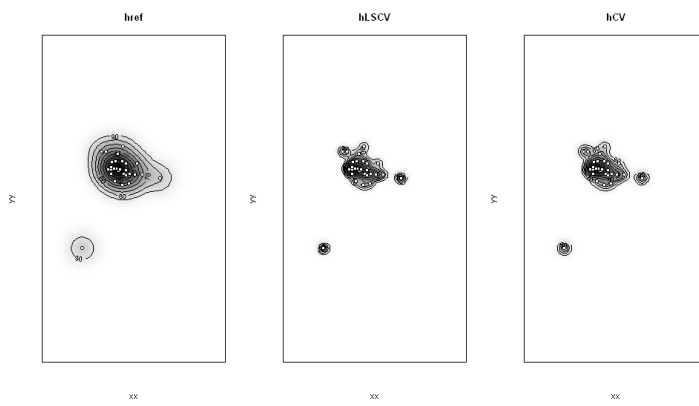
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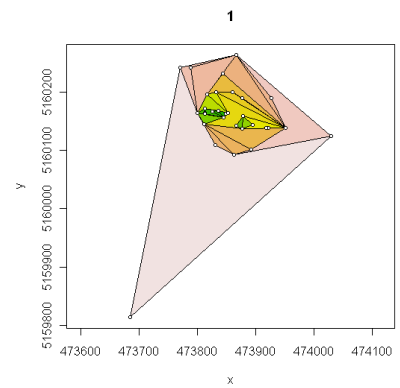
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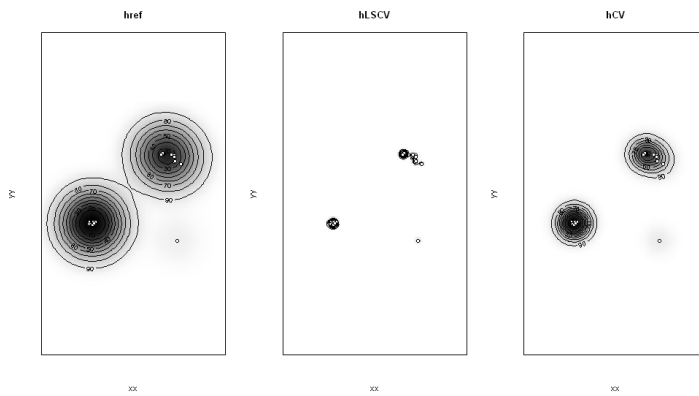
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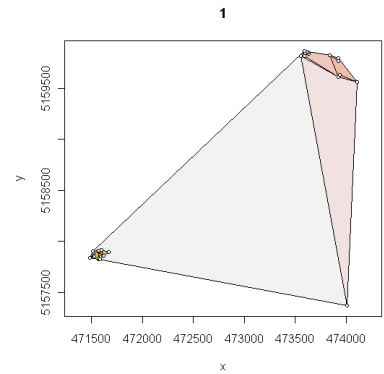
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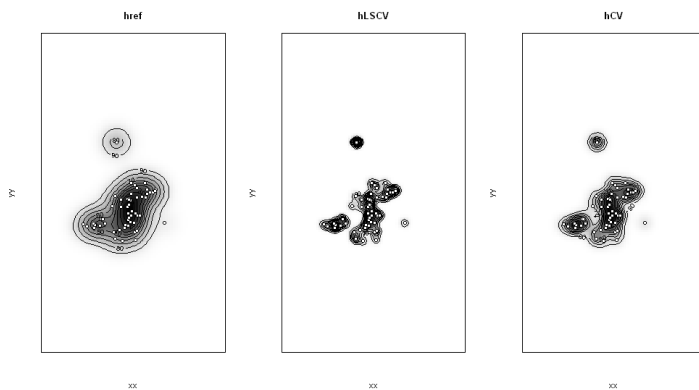
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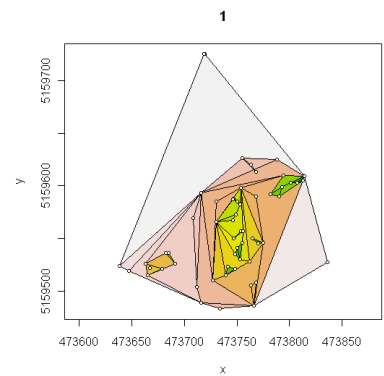
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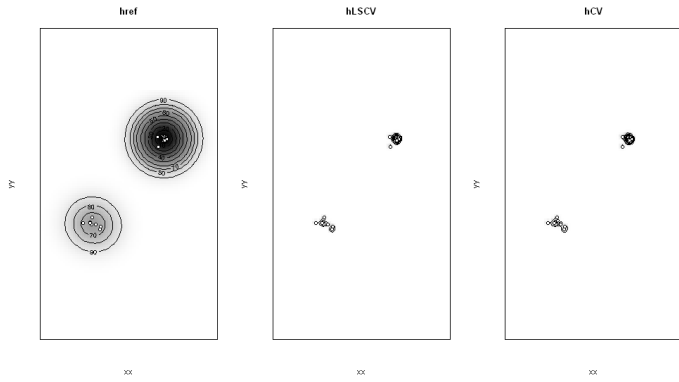
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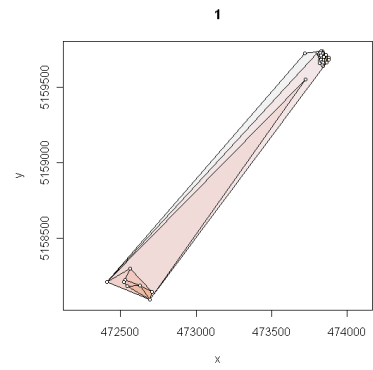
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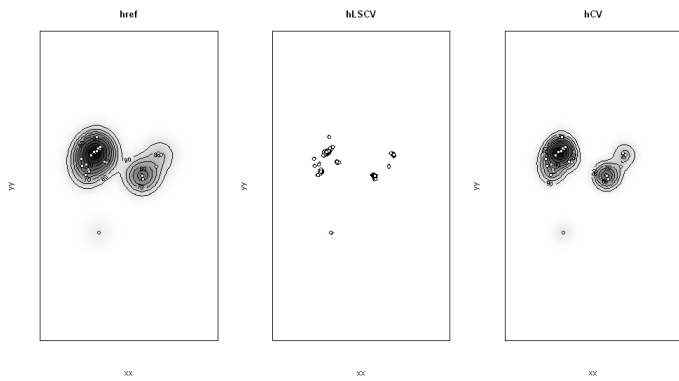
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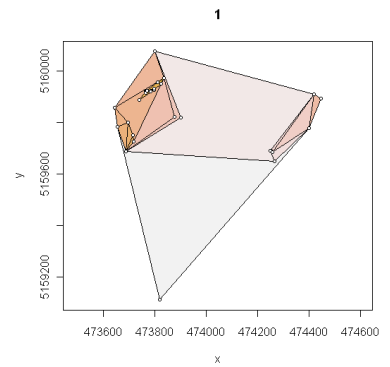
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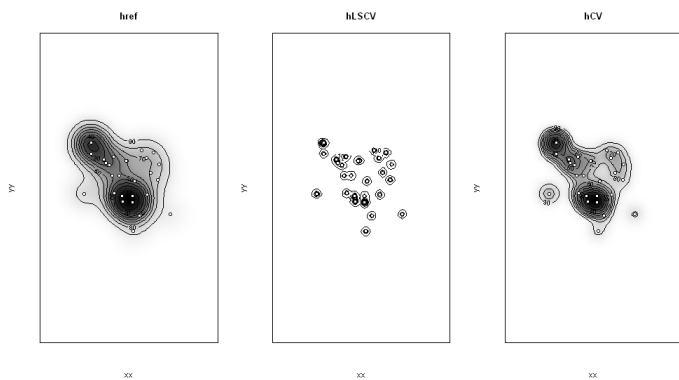
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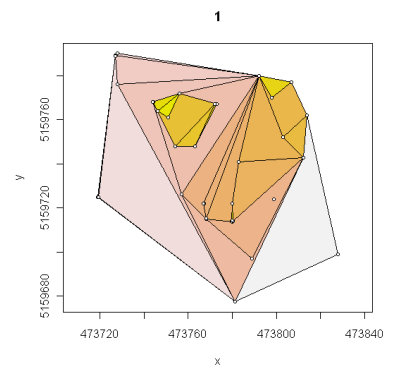
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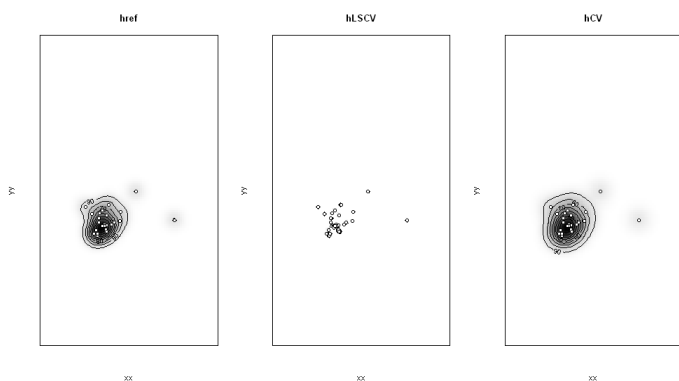
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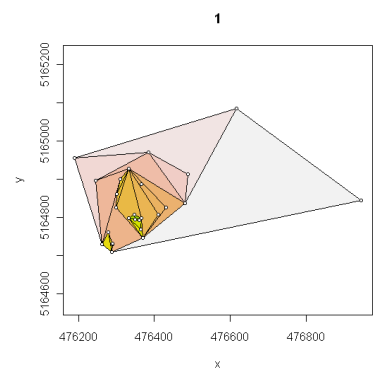
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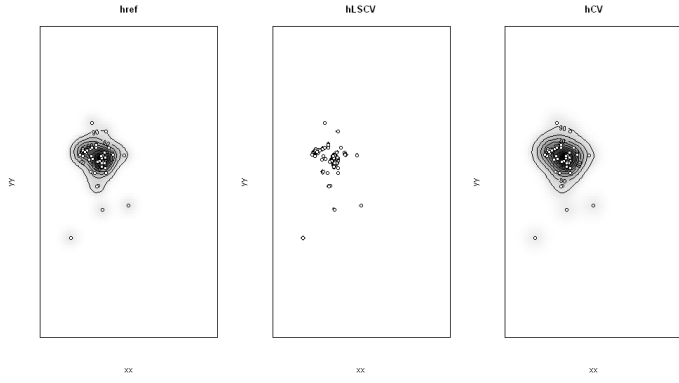
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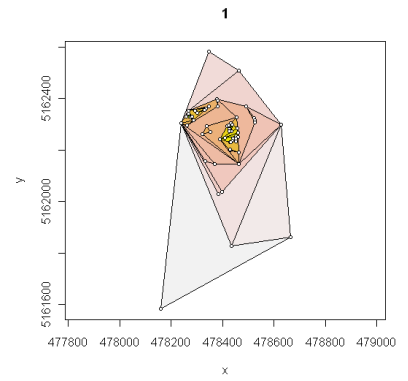
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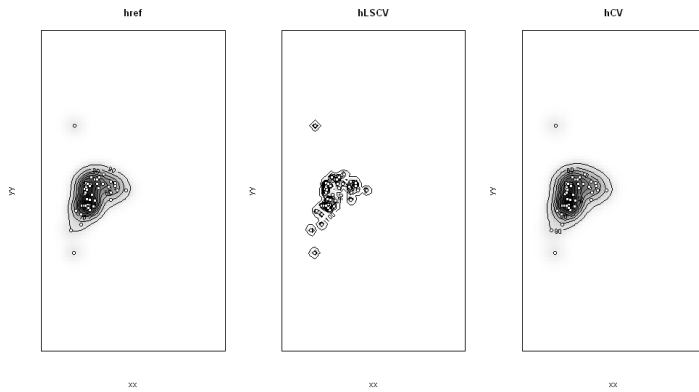
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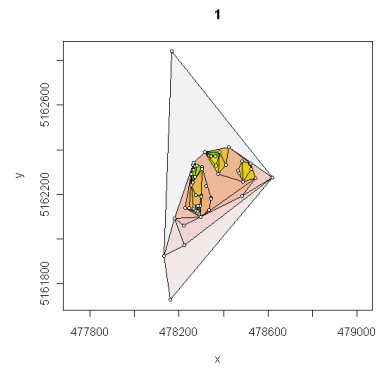
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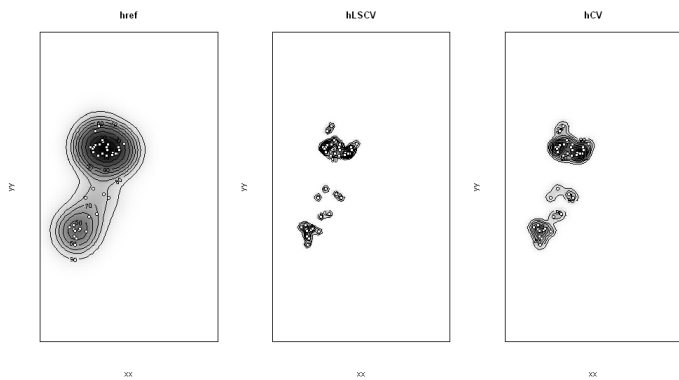
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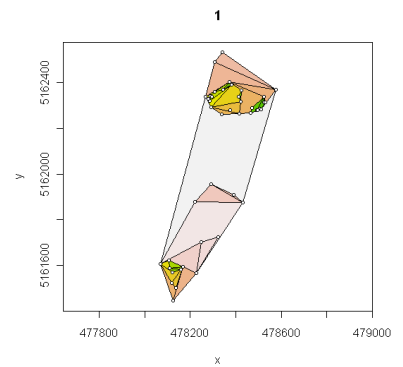
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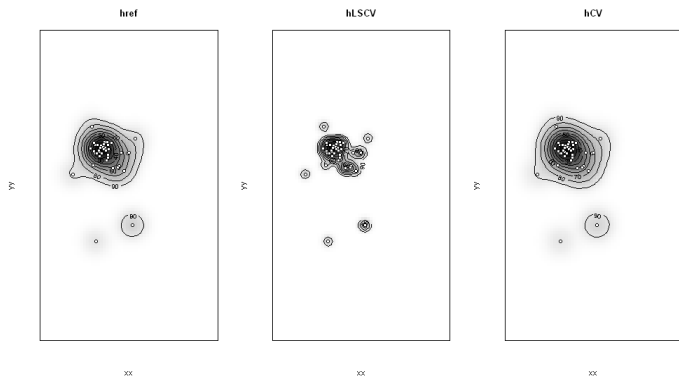
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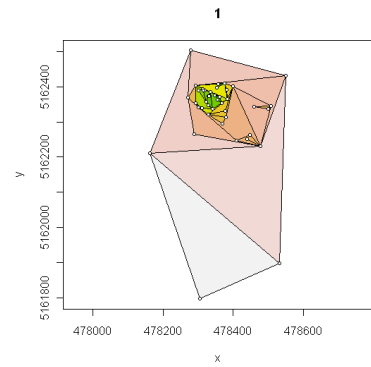
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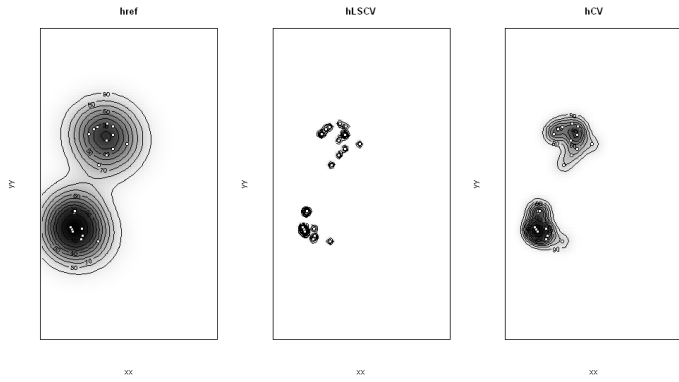
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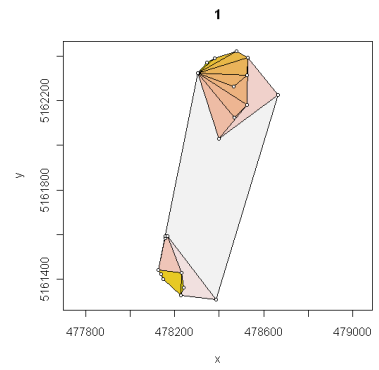
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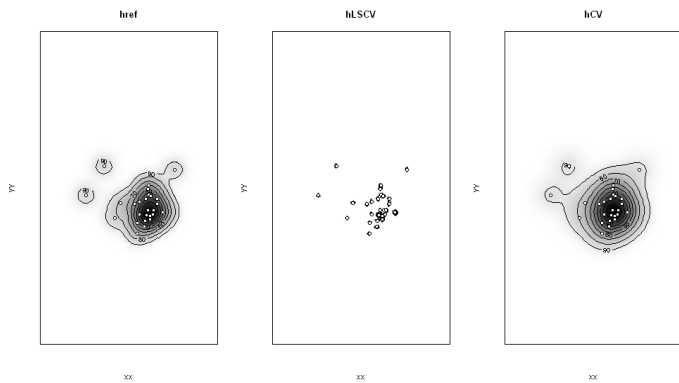
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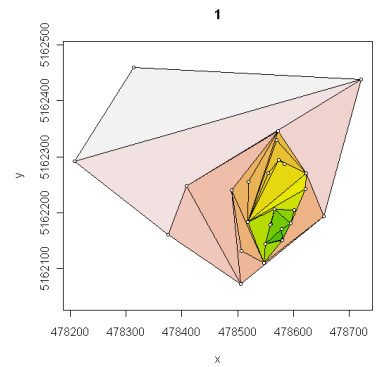
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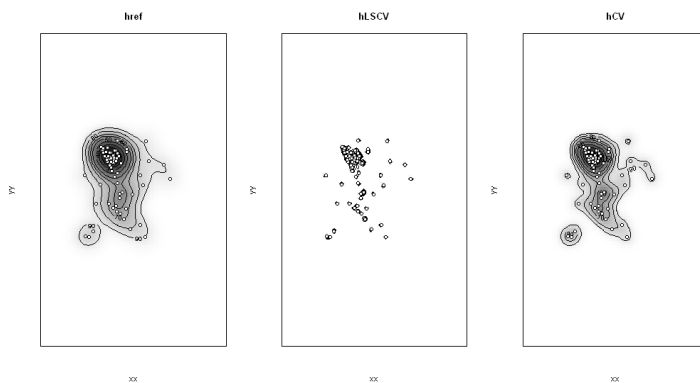
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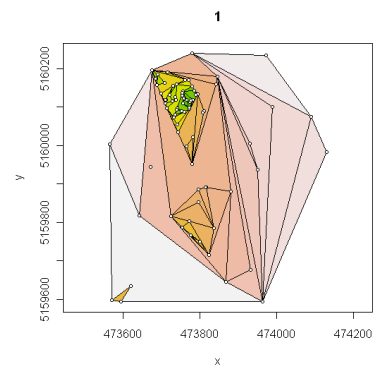
href (2CN), DV multimodal : ICP



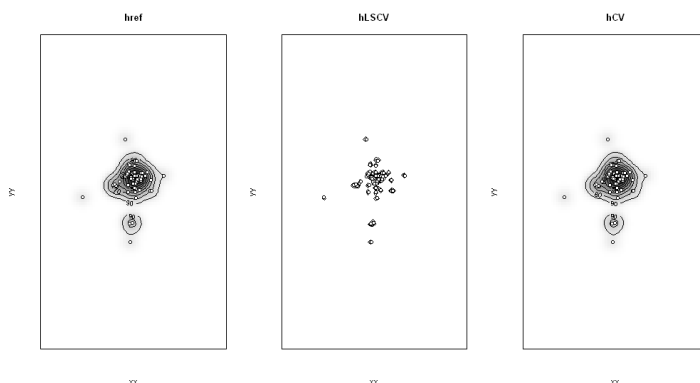
2Mbe2008-3-F-A-618 (locs : 90)



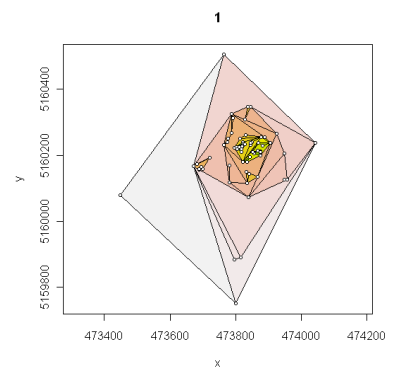
hcv (2BVN), DV multimodal : ICP



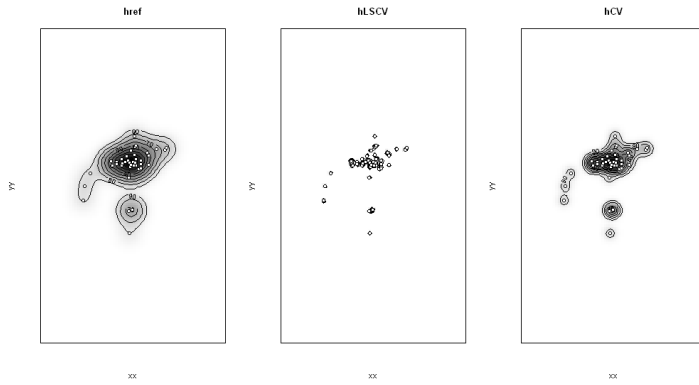
2Mbe2008-3-F-A-778 (locs : 76)



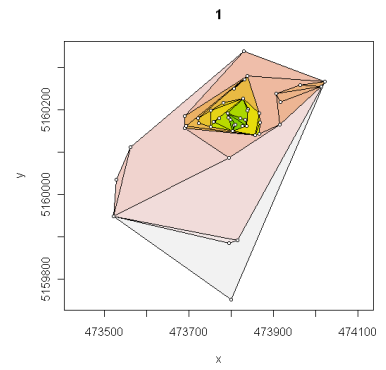
href-hcv (2BVN), DV multimodal : ICP



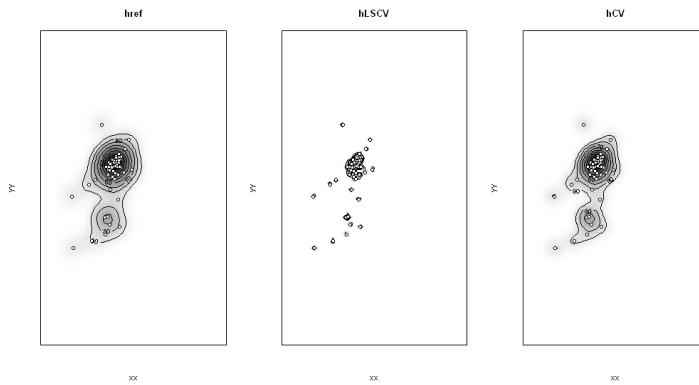
2Mbe2008-3-F-A-818 (locs : 56)



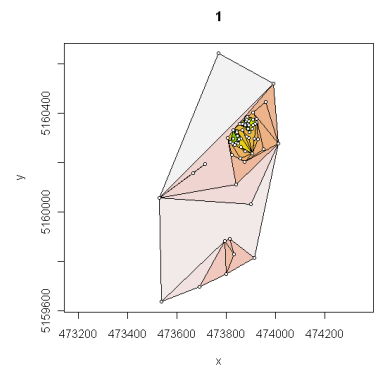
hcv (2BVN), DV multimodal : ICP



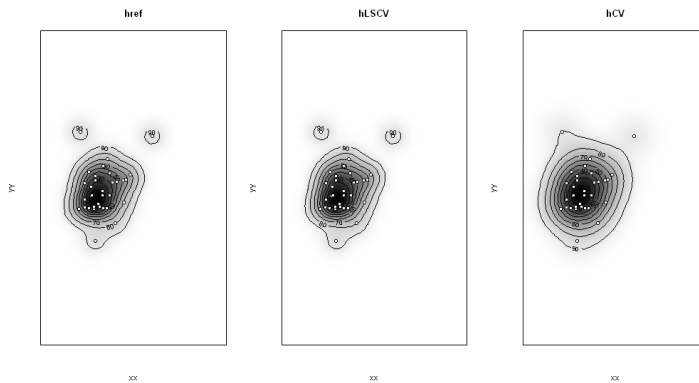
2Mbe2008-3-F-A-858 (locs : 73)



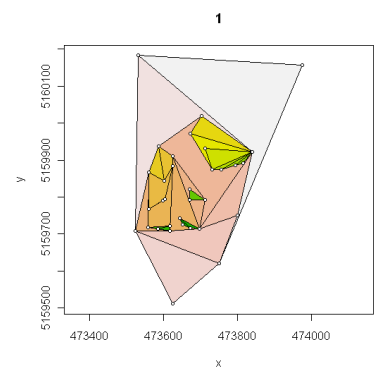
hLscv-(hcv) (2BVN), DV multimodal : ICP



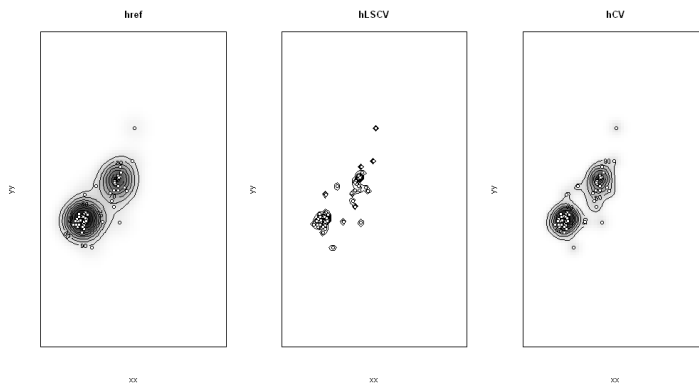
2Mbe2008-3-F-A-898 (locs : 35)



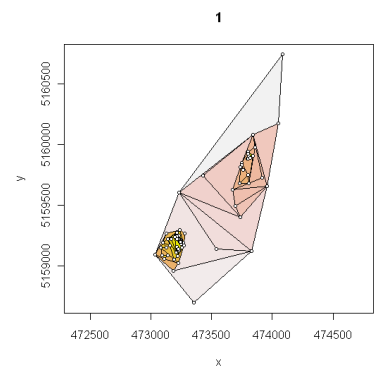
(hcv) (BVN), DV bimodal : ICP



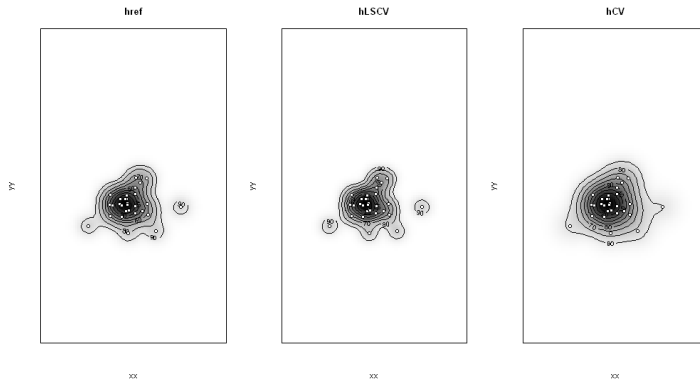
2Mbe2008-3-F-J-758 (locs : 79)



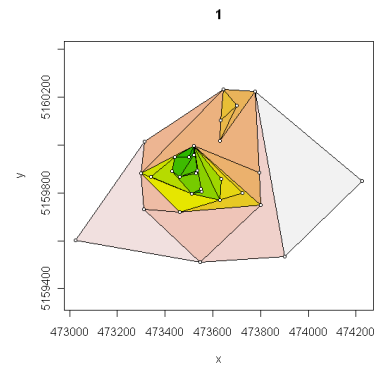
hcv (2BVN), DV multimodal : ICP



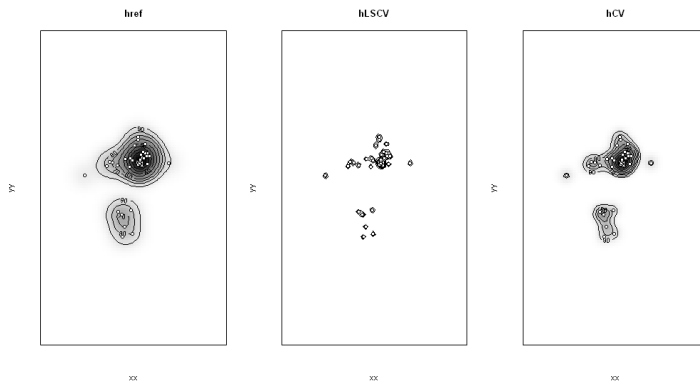
2Mbe2008-3-F-J-918 (locs : 31)



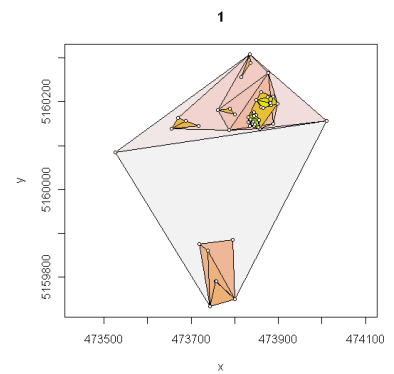
hLscv (2CN), DV multimodal : ICP



2Mbe2008-3-M-J-718 (locs : 60)



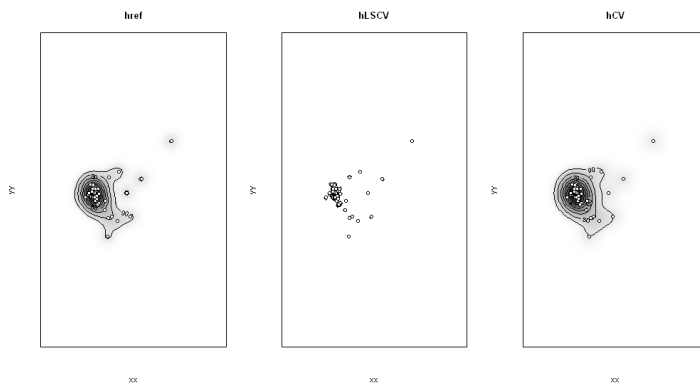
hcv (2BVN), DV multimodal : ICP



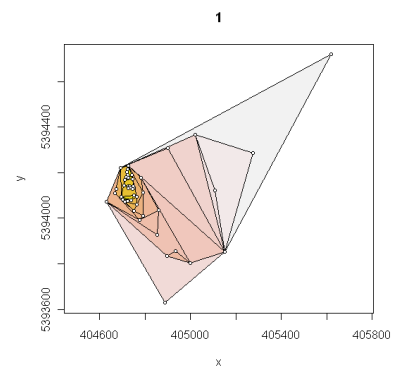
*Myotis nattereri*

Site : Forêt Domaniale de Rambouillet

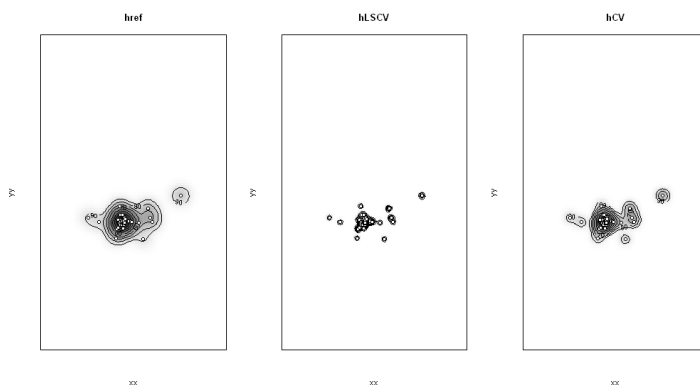
1Mna2009-2-F-A-119 (locs : 63)



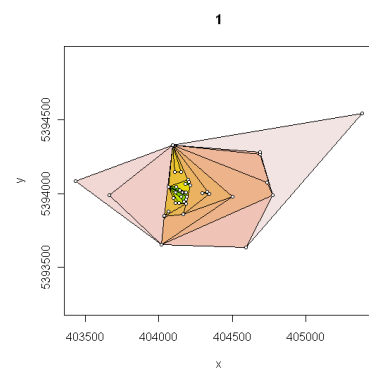
href (2BVN), DV multimodal : ICP



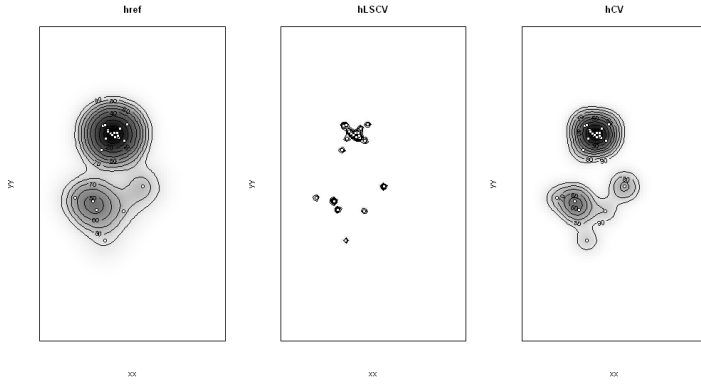
1Mna2009-2-F-A-139 (locs : 43)



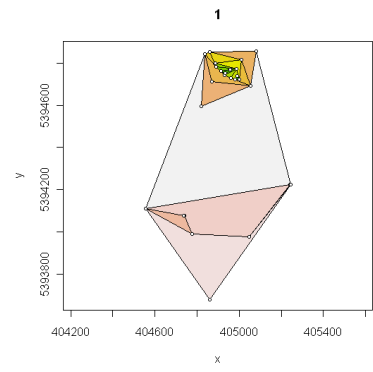
hcv (2CN), DV multimodal : ICP



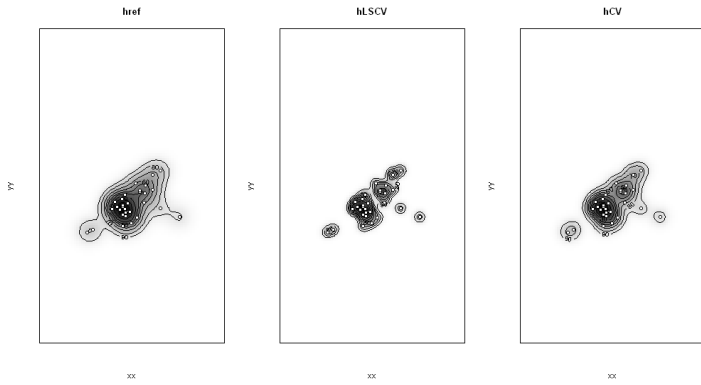
1Mna2009-2-F-A-158 (locs : 29)



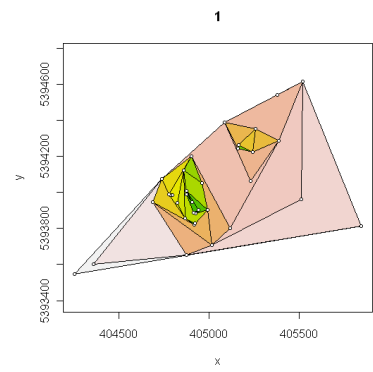
hcv (2CN), DV multimodal : ICP



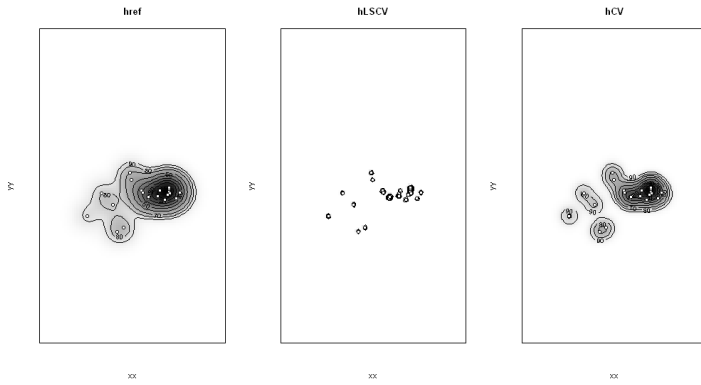
1Mna2009-2-F-A-179 (locs : 38)



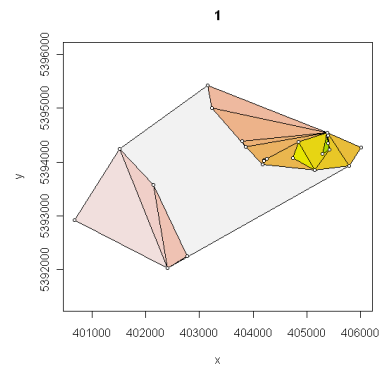
hLscv (2CN), DV multimodal : ICP



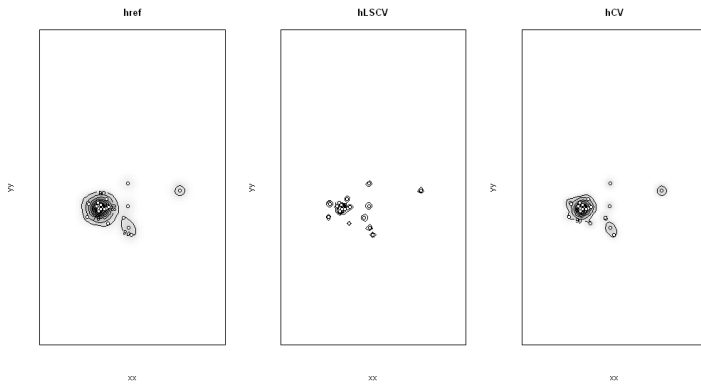
1Mna2009-2-F-A-219 (locs : 29)



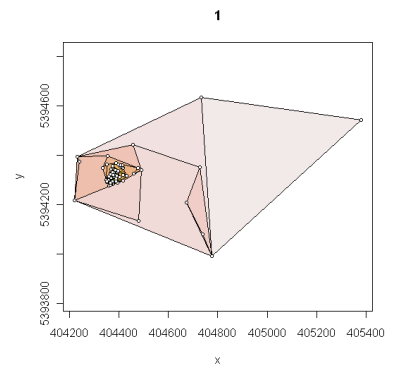
hcv (2BVN), DV multimodal : ICP



1Mna2009-2-F-A-238 (locs : 76)

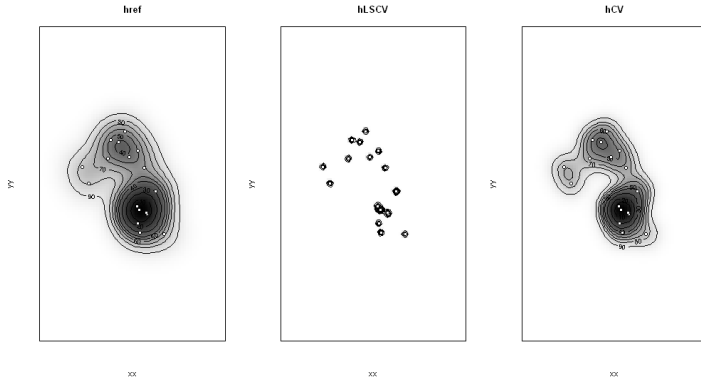


hcv (2BVN), DV multimodal : ICP

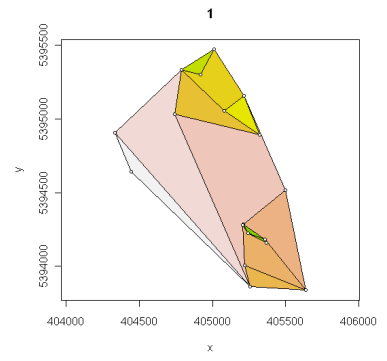




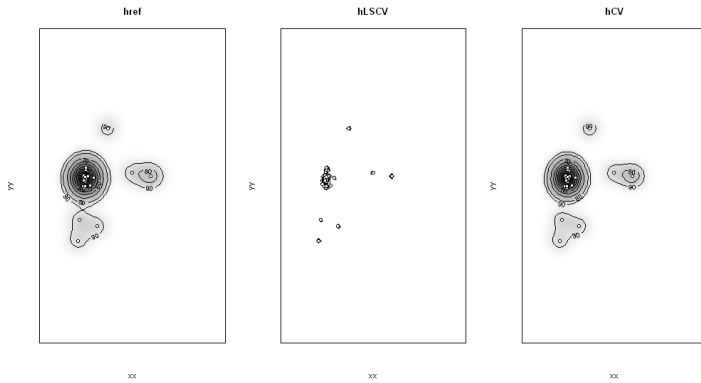
1Mna2009-2-F-A-398 (locs : 23)



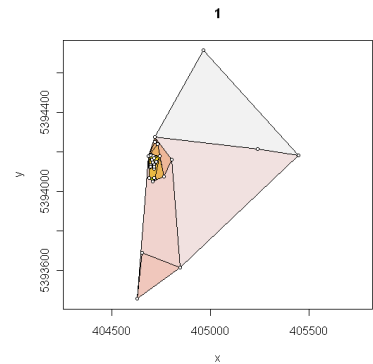
hcv (2CN), DV multimodal : ICP



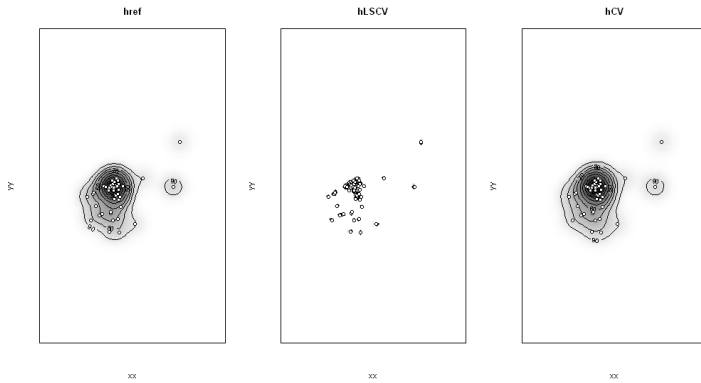
1Mna2009-3-F-A-697 (locs : 40)



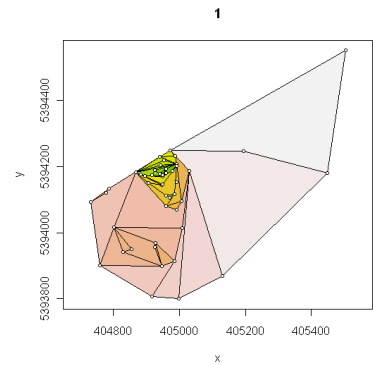
hcv (2BVN), DV multimodal : ICP



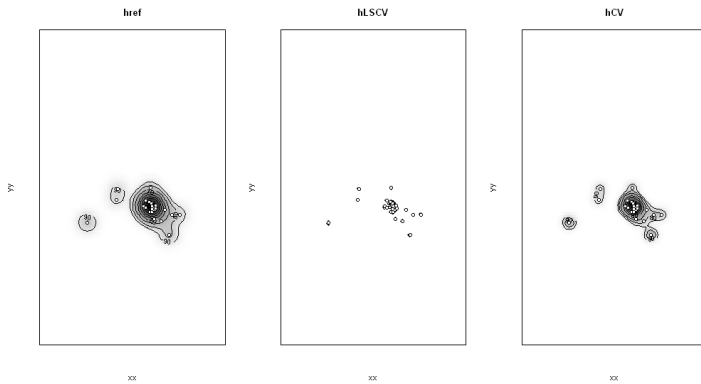
1Mna2009-3-F-A-858 (locs : 59)



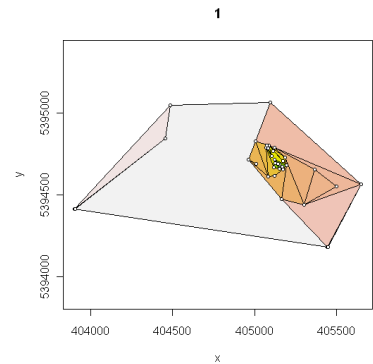
(href) (2CN), DV multimodal : ICP



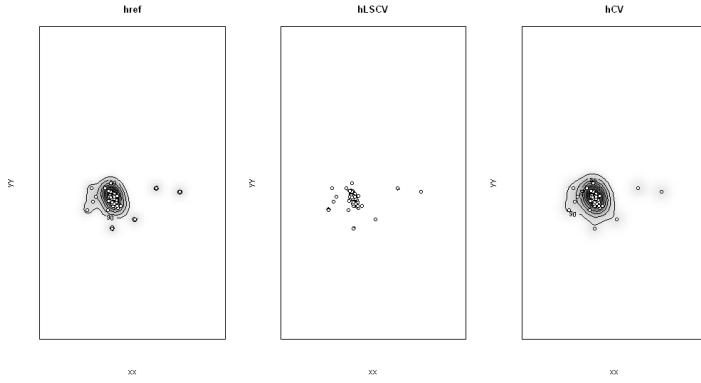
1Mna2009-3-F-J-418 (locs : 44)



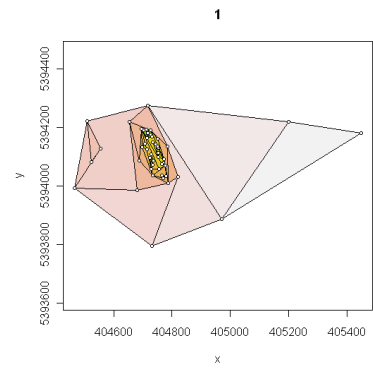
hcv (2BVN), DV multimodal : ICP



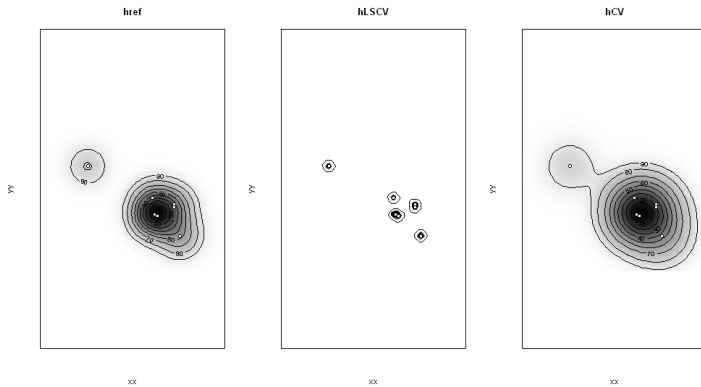
1Mna2009-3-F-J-458 (locs : 56)



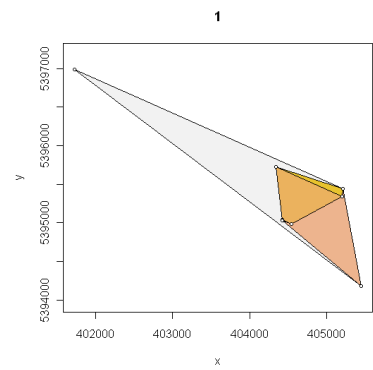
href (CU), DV unimodal : MCP



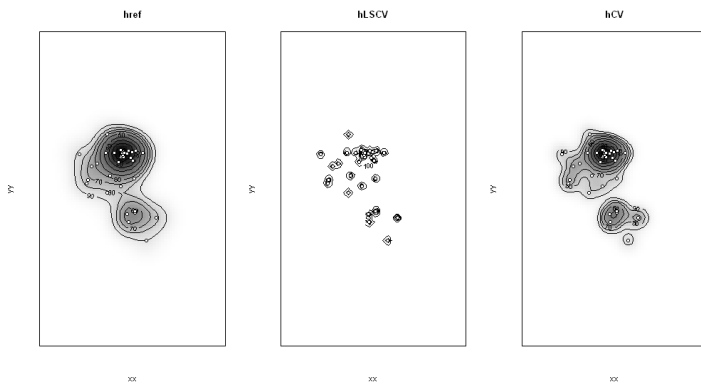
1Mna2009-3-F-J-497 (locs : 12)



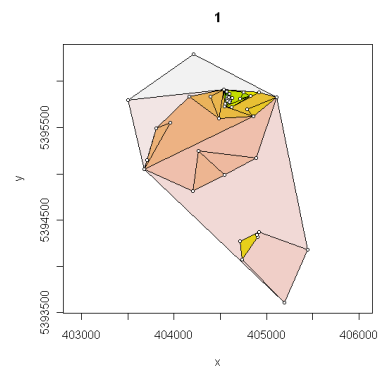
(href) (2BVN), DV multimodal : ICP



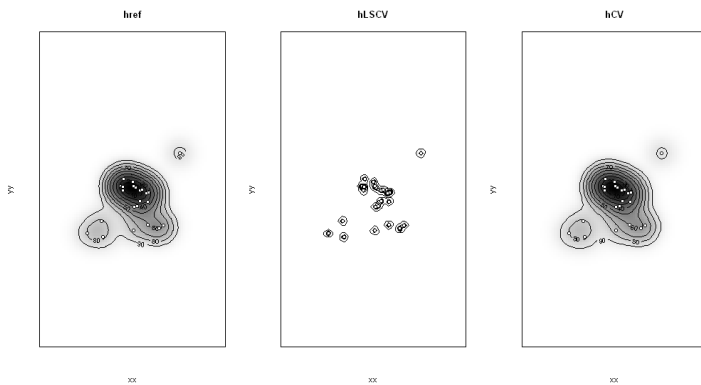
1Mna2009-3-F-J-599 (locs : 48)



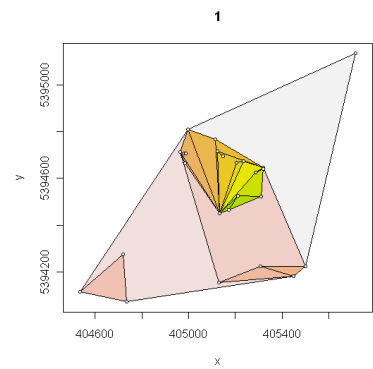
hcv (2BVN), DV multimodal : ICP



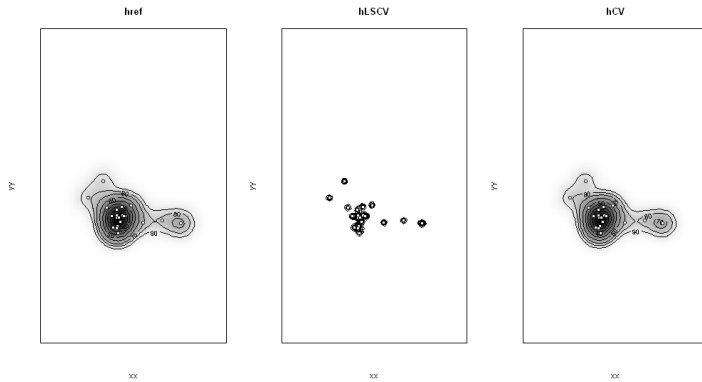
1Mna2009-3-F-J-658 (locs : 31)



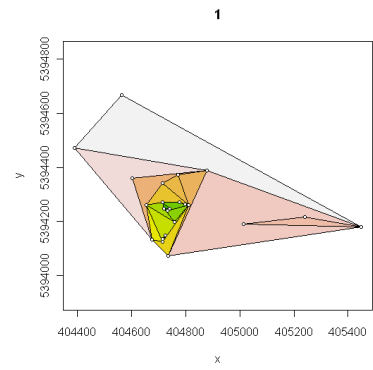
href (2BVN), DV multimodal : ICP



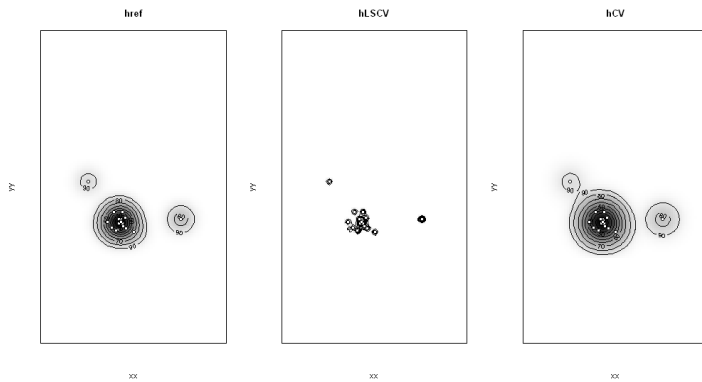
1Mna2009-3-F-J-677 (locs : 25)



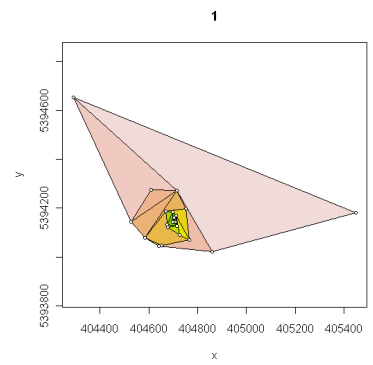
(hcv) (2CN), DV multimodal : ICP



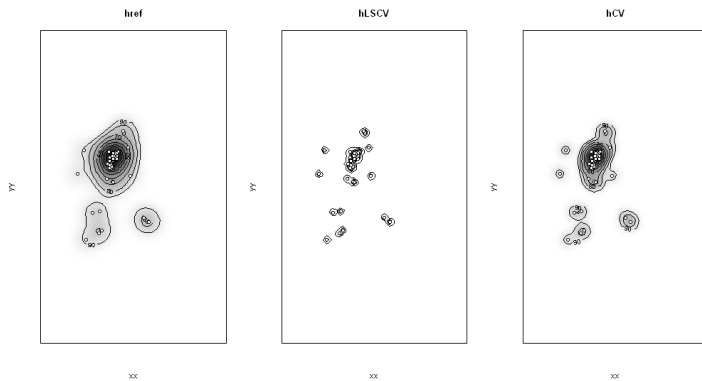
1Mna2009-3-F-J-898 (locs : 23)



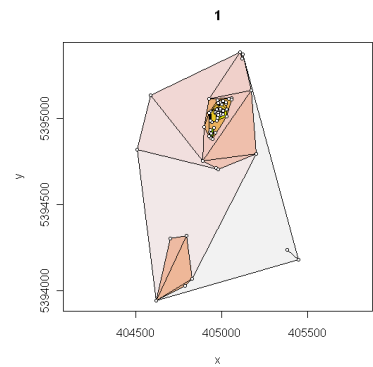
(href) (2CN), DV multimodal : ICP



1Mna2009-3-F-J-918 (locs : 66)



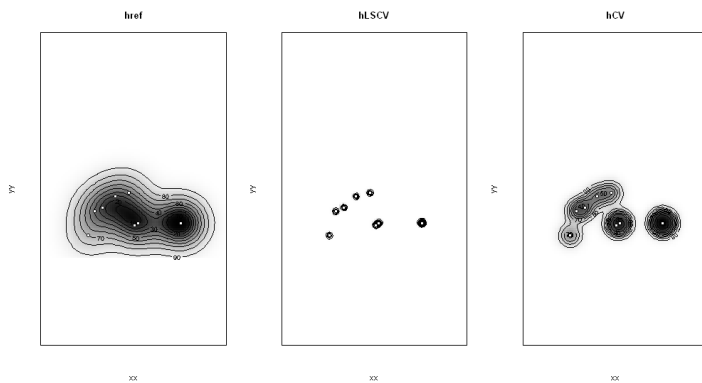
hcv (2BVN), DV multimodal : ICP



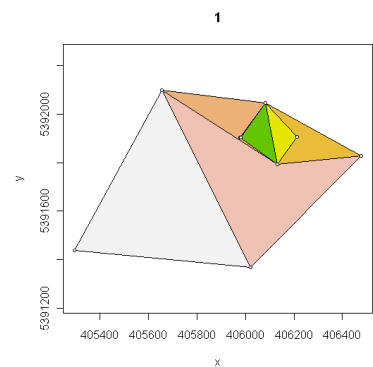
*Plecotus auritus*

Site : Forêt Domaniale de Rambouillet

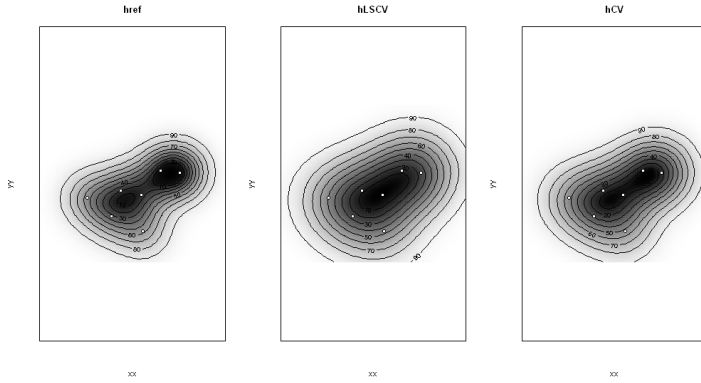
1Paur2006-1-F-A-179 (locs : 12)



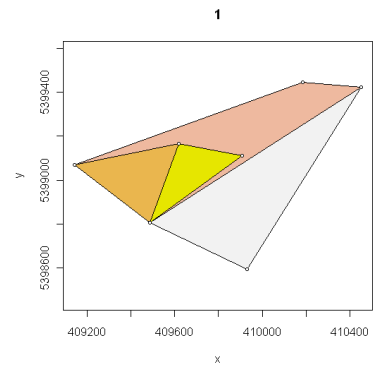
hcv (2BVN), DV multimodal : ICP



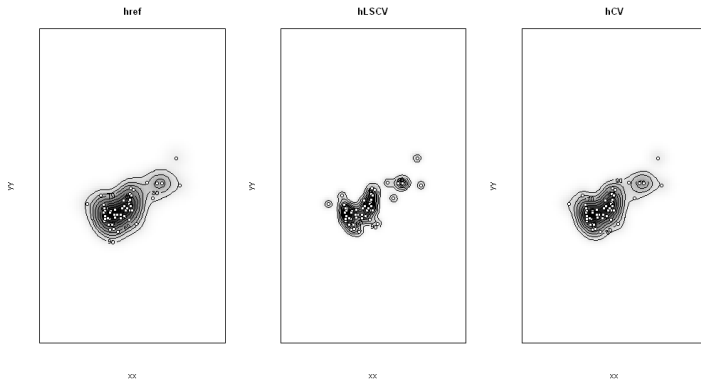
1Paur2006-1-F-A-419 (locs : 8)



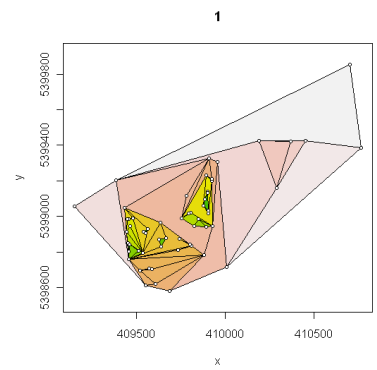
(href) (2CN), DV multimodal : ICP



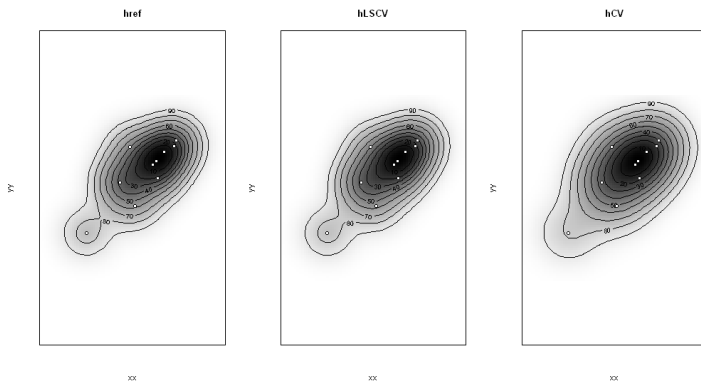
1Paur2006-1-F-A-438 (locs : 61)



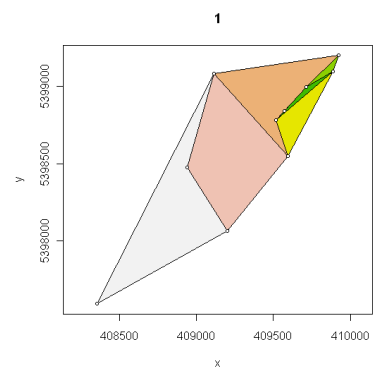
hLscv (2BVN), DV multimodal : ICP



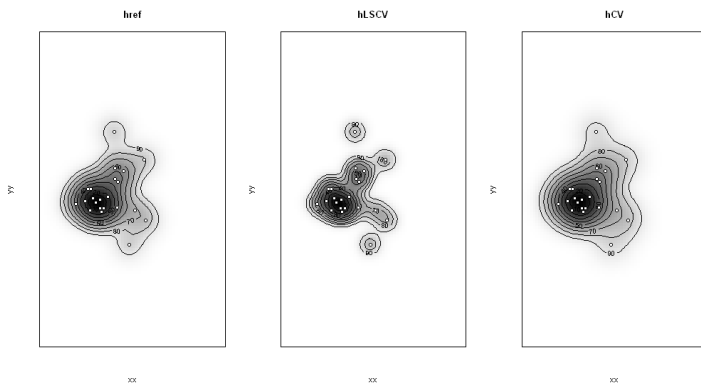
1Paur2006-1-F-A-458 (locs : 11)



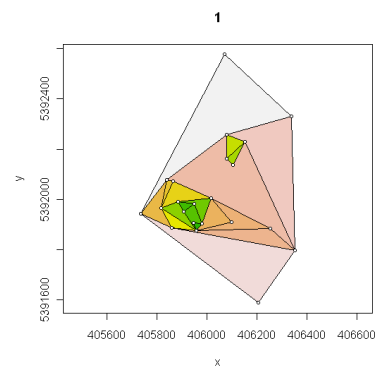
(href) (2BVN), DV multimodal : ICP



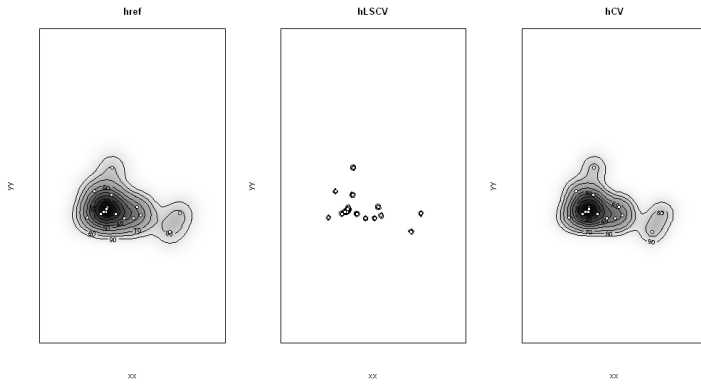
1Paur2006-1-M-A-118 (locs : 24)



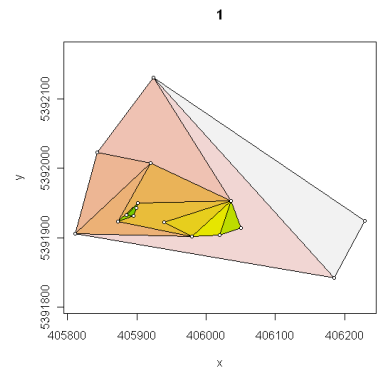
hLscv (2CN), DV multimodal : ICP



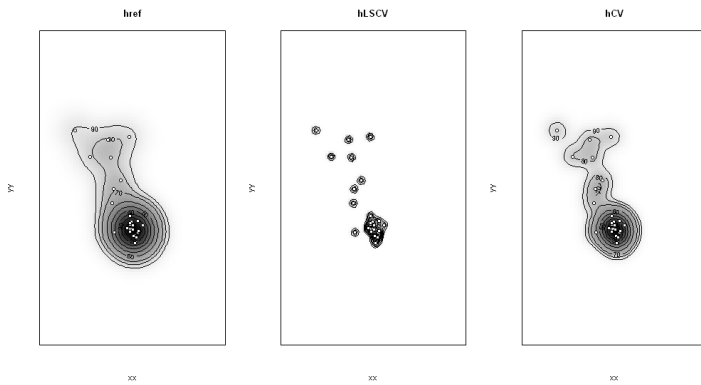
1Paur2006-1-M-A-138 (locs : 19)



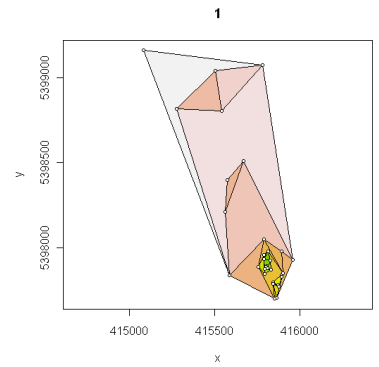
hcv (2CN), DV multimodal : ICP



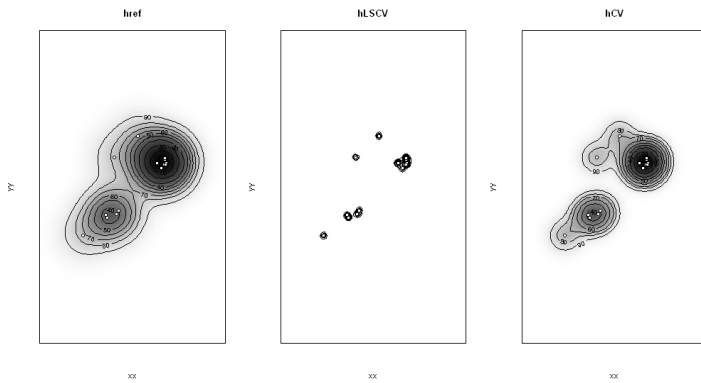
1Paur2006-1-M-A-278 (locs : 33)



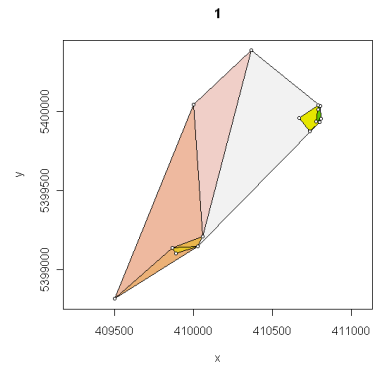
hcv (2CN), DV multimodal : ICP



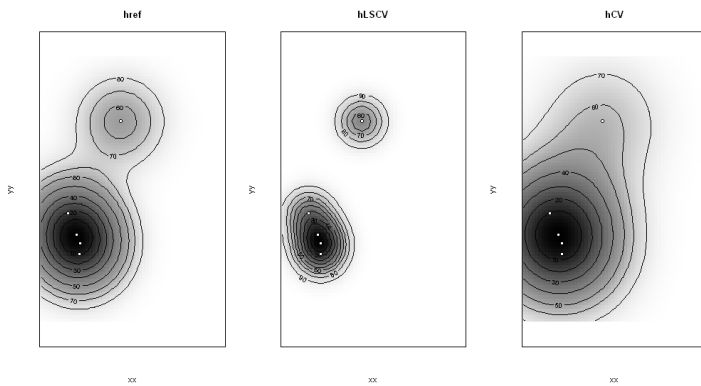
1Paur2006-2-F-A-498 (locs : 16)



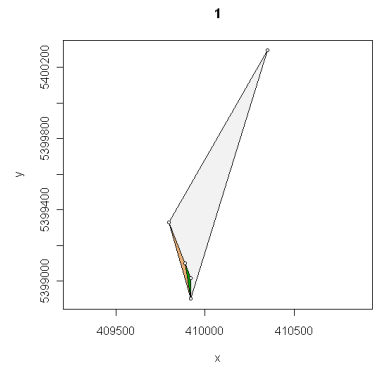
hcv (2CN), DV multimodal : ICP



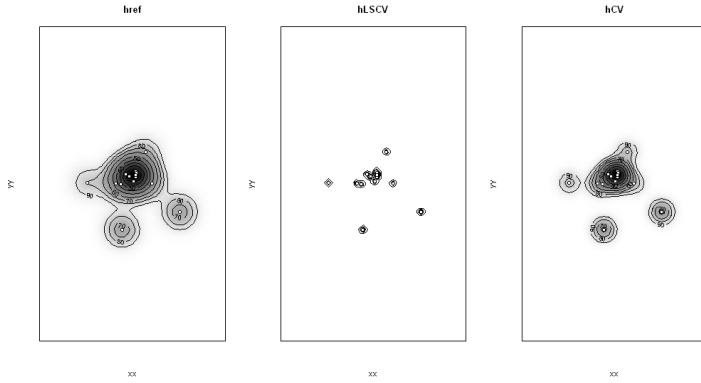
1Paur2006-2-F-A-798 (locs : 5)



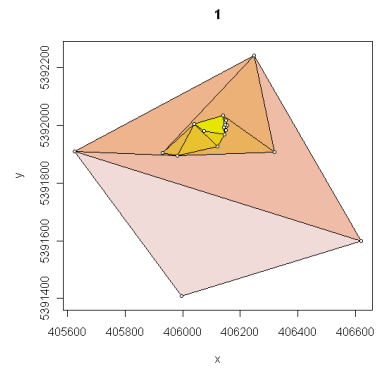
(href) (2BVN), DV multimodal : ICP



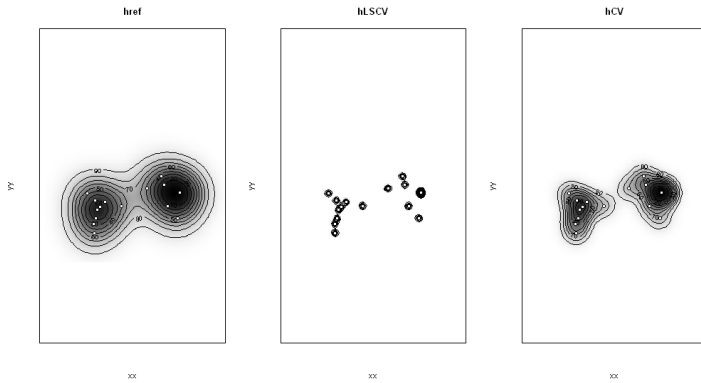
1Paur2006-2-F-A-838 (locs : 22)



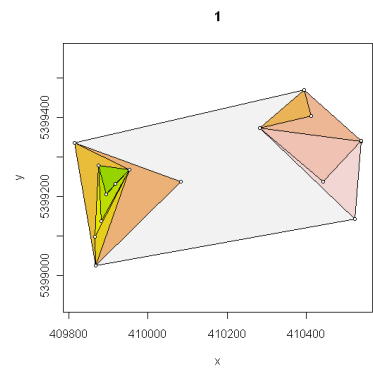
hcv (2CN), DV multimodal : ICP



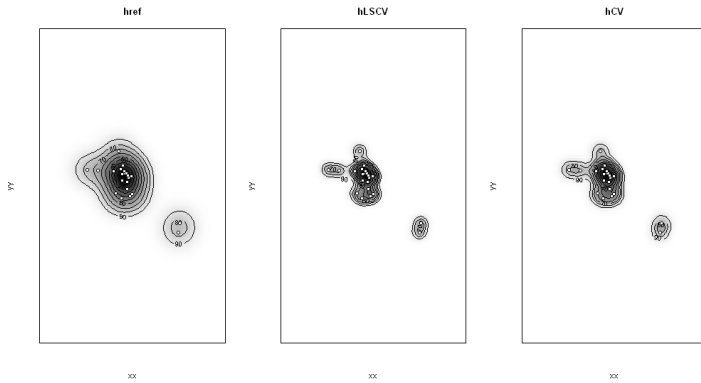
1Paur2006-2-M-A-198 (locs : 20)



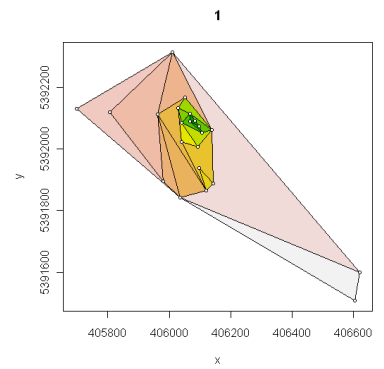
(hcv) (2CN), DV multimodal : ICP



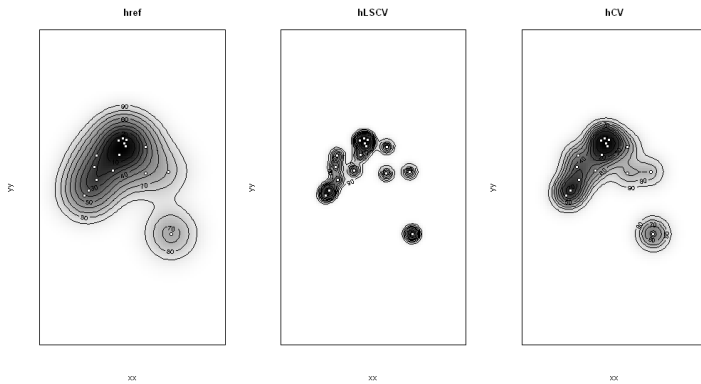
1Paur2006-2-M-A-898.2 (locs : 22)



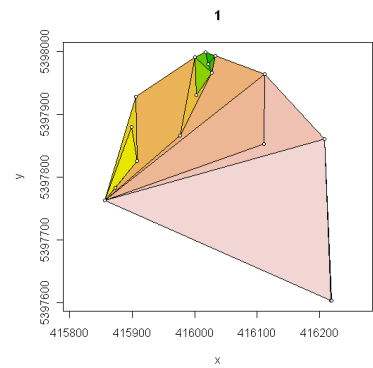
hcv (BVN), DV bimodal : ICP



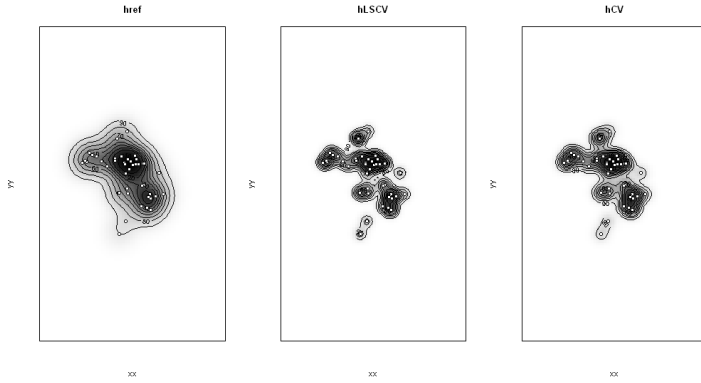
1Paur2006-3-F-A-858 (locs : 18)



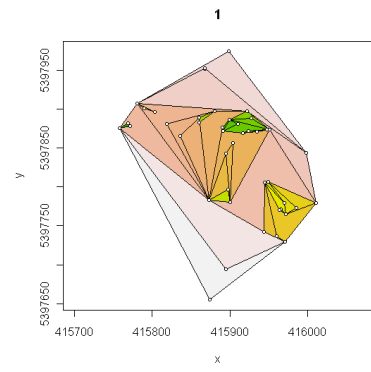
hcv (2CN), DV multimodal : ICP



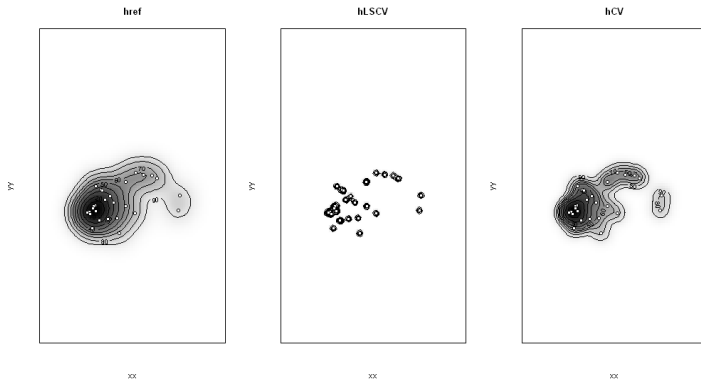
1Paur2006-3-M-A-877 (locs : 47)



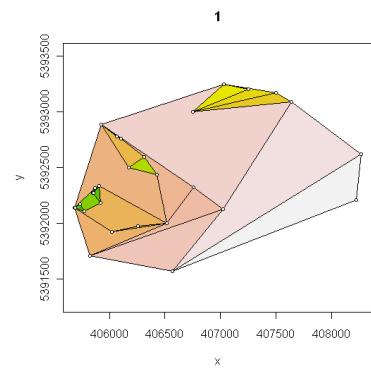
hlscv (2CN), DV multimodal : ICP



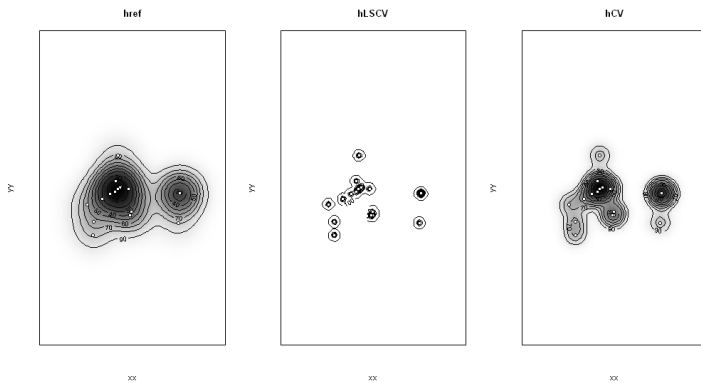
1Paur2006-3-M-J-537 (locs : 32)



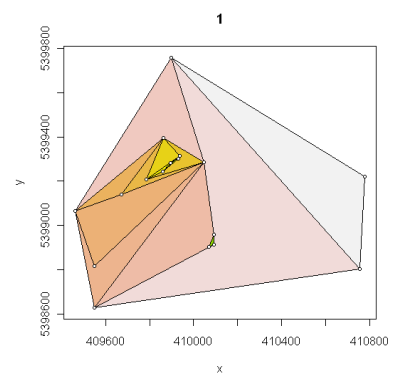
hcv (2CN), DV multimodal : ICP



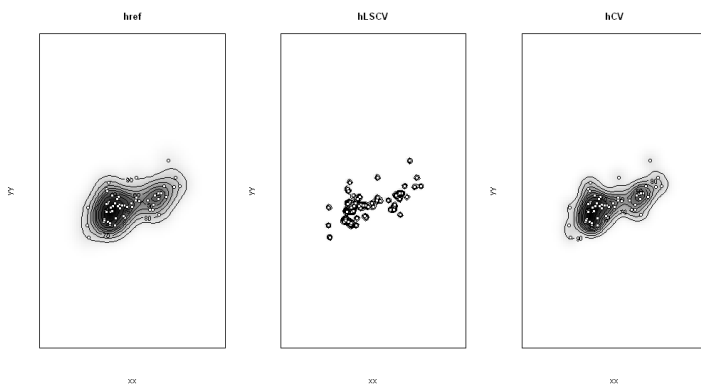
1Paur2007-1-F-A-058 (locs : 25)



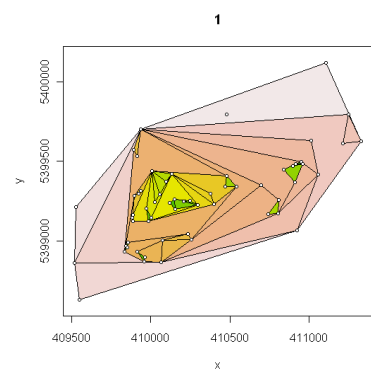
hcv (2BVN), DV multimodal : ICP



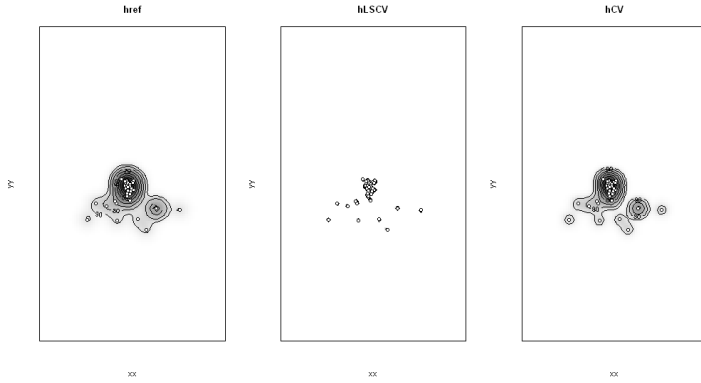
1Paur2007-1-F-A-078 (locs : 65)



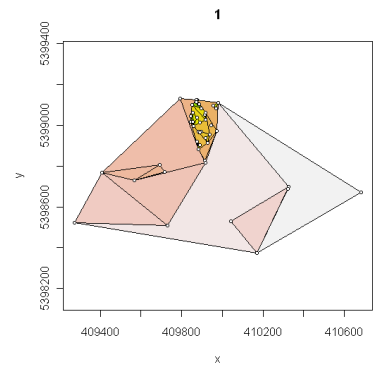
(hcv) (2CN), DV multimodal : ICP



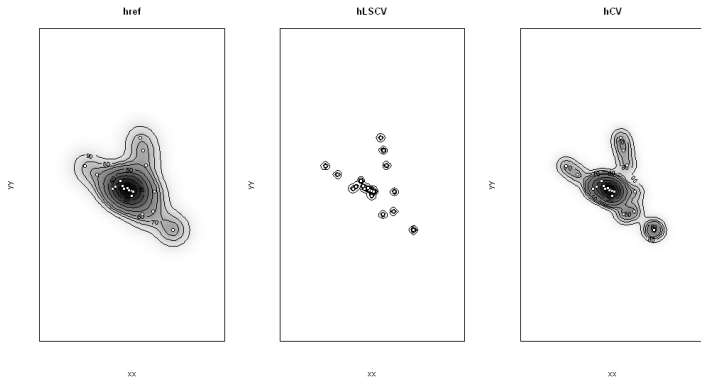
1Paur2007-2-F-A-118 (locs : 52)



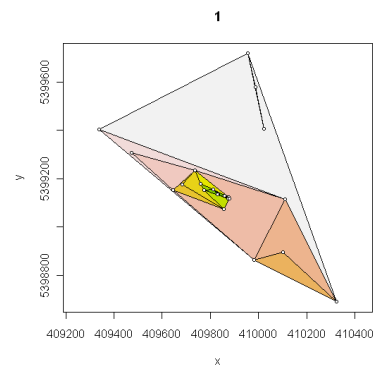
hcv (2BVN), DV multimodal : ICP



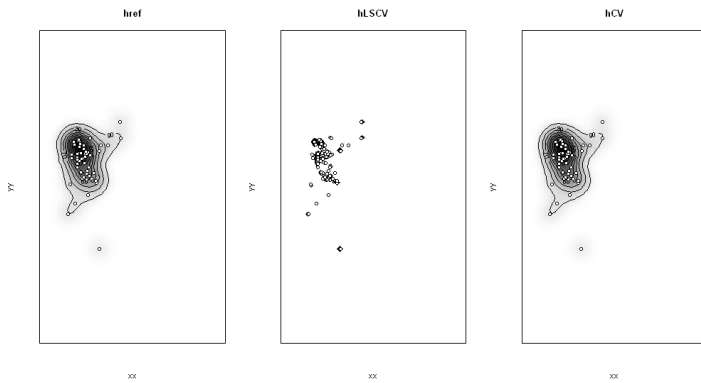
1Paur2007-2-M-A-100 (locs : 24)



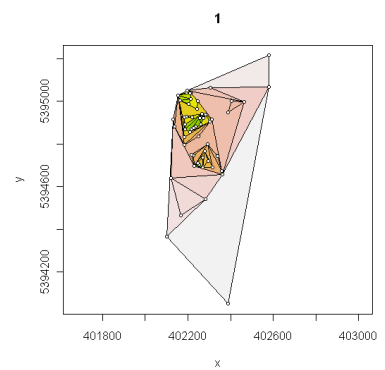
(href) (BVN), DV bimodal : ICP



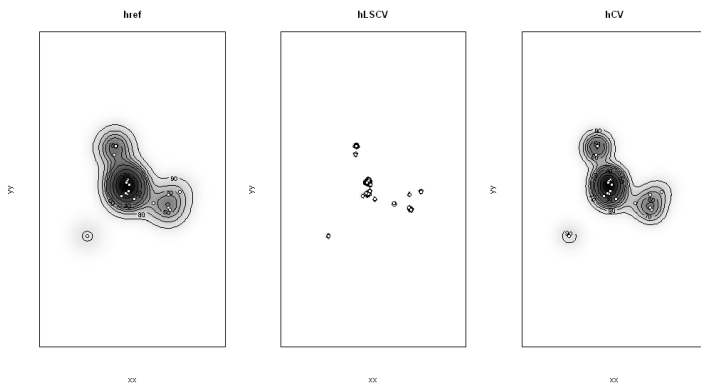
1Paur2009-1-F-A-055 (locs : 68)



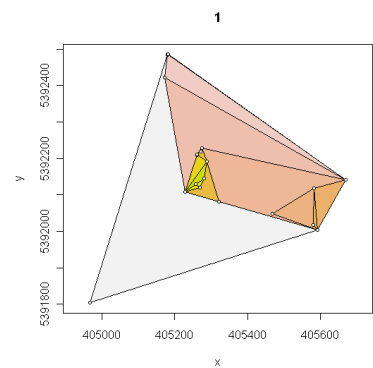
(href-hcv) (2BVN), DV multimodal : ICP



1Paur2009-1-F-A-096 (locs : 27)

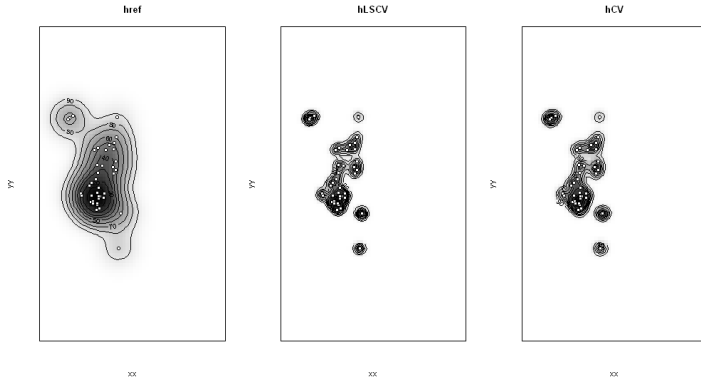


hcv (2CN), DV multimodal : ICP

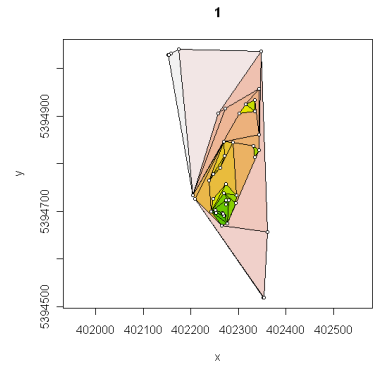




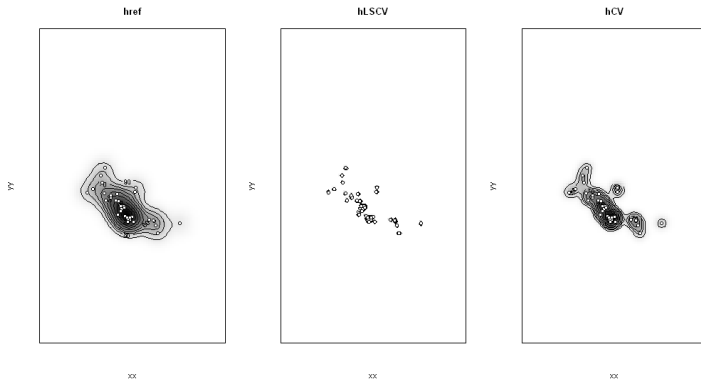
1Paur2009-1-F-A-355 (locs : 46)



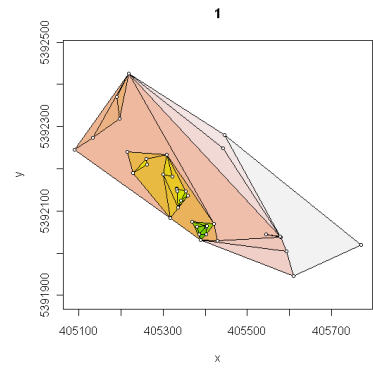
hLscv (2BVN), DV multimodal : ICP



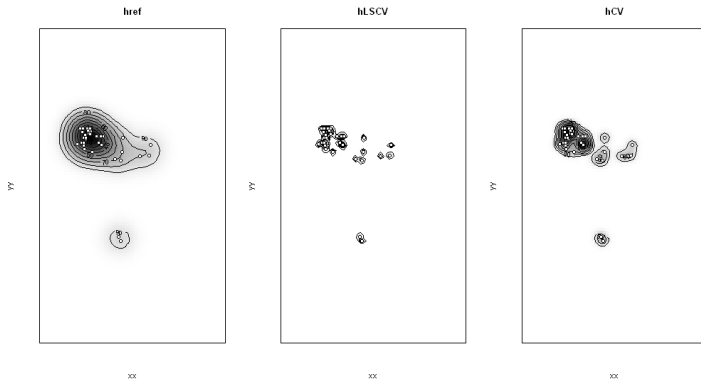
1Paur2009-1-F-A-696 (locs : 40)



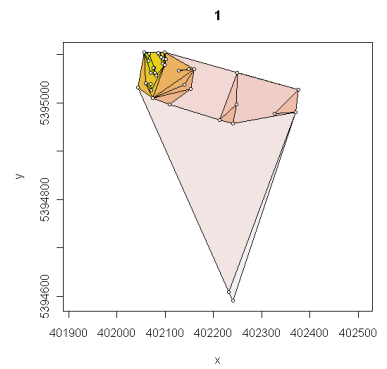
hcv (BVN), DV bimodal : ICP



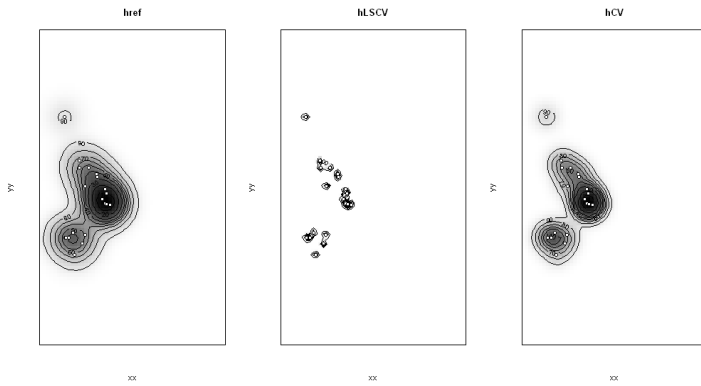
1Paur2009-1-F-A-897 (locs : 43)



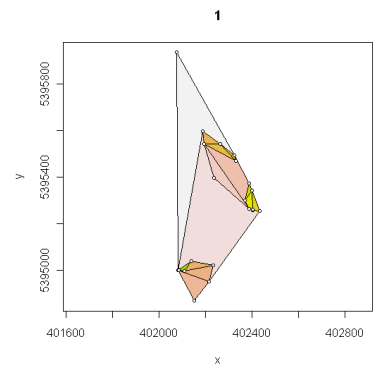
hcv (2CN), DV multimodal : ICP



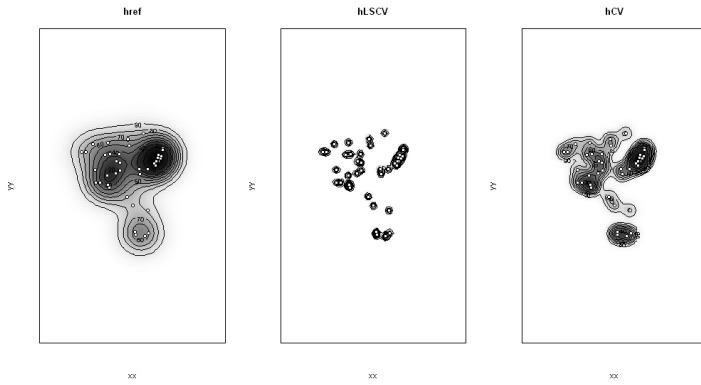
1Paur2009-1-F-A-977 (locs : 27)



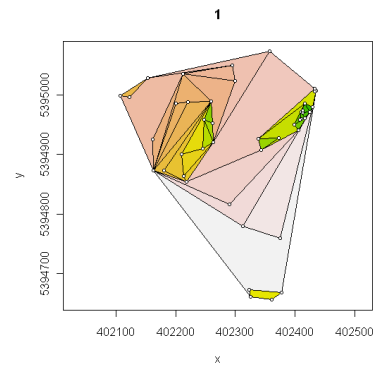
hcv (2BVN), DV multimodal : ICP



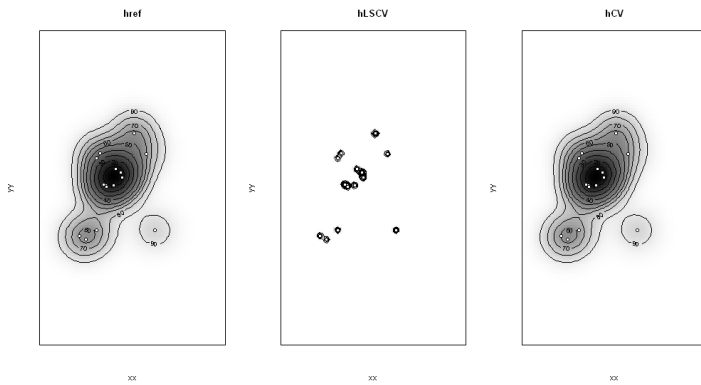
1Paur2009-1-M-A-037 (locs : 49)



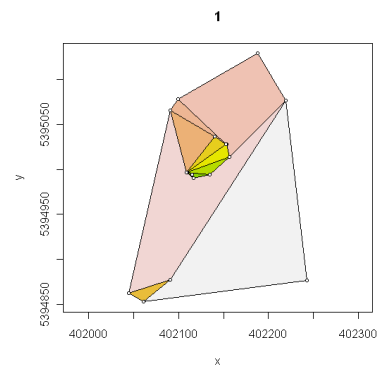
hcv (2BVN), DV multimodal : ICP



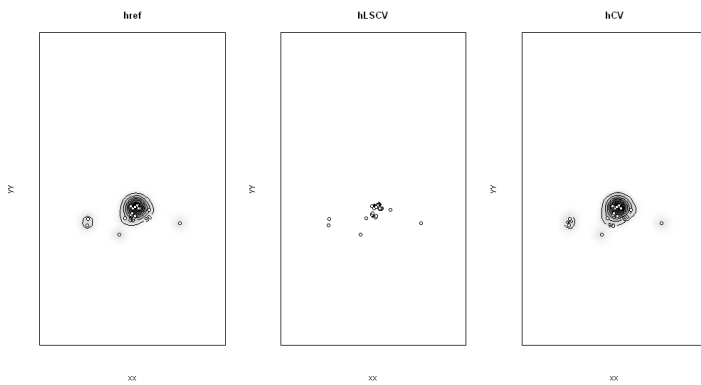
1Paur2009-1-M-A-857 (locs : 20)



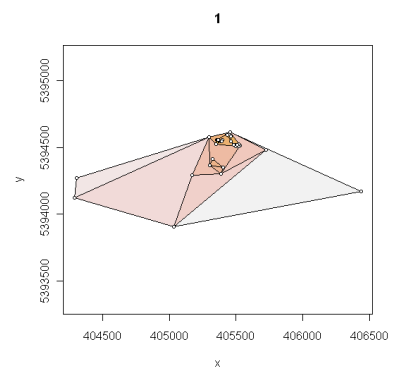
href-hcv (2CN), DV bimodal : ICP



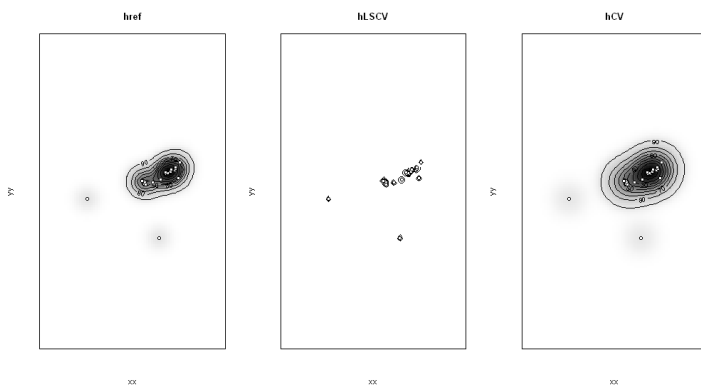
1Paur2009-2-F-A-038 (locs : 48)



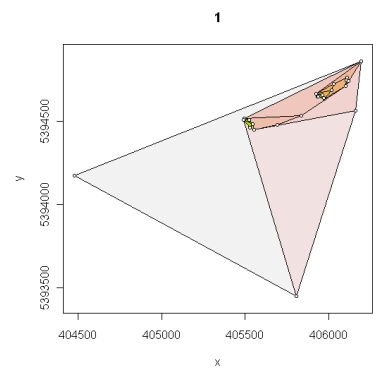
href (2BVN), DV multimodal : ICP



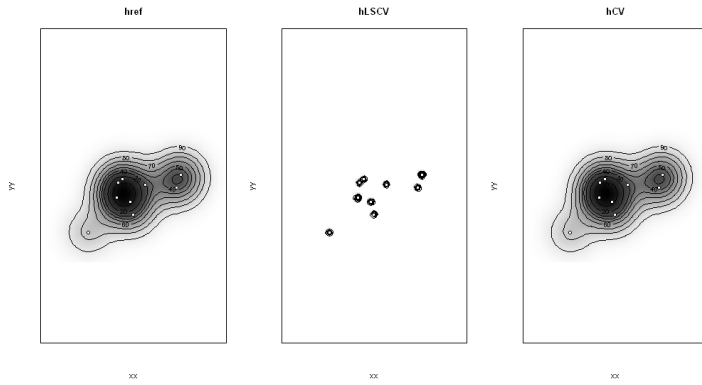
1Paur2009-2-F-A-058 (locs : 35)



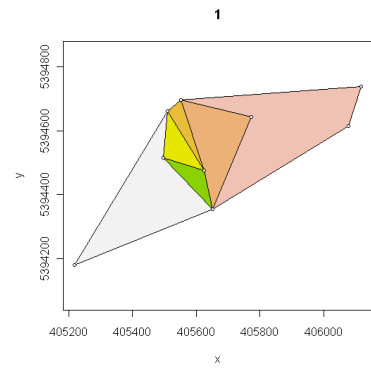
(href) (2BVN), DV multimodal : ICP



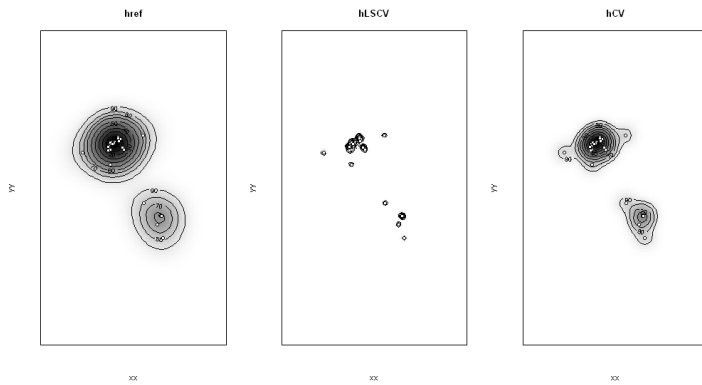
1Paur2009-2-F-A-077 (locs : 11)



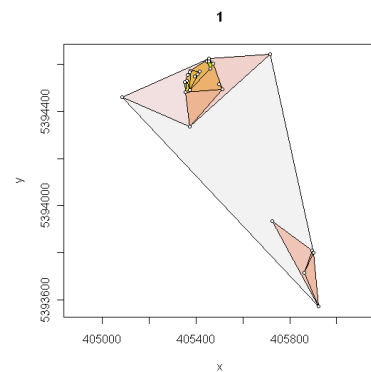
(href-hcv) (2BVN), DV multimodal : ICP



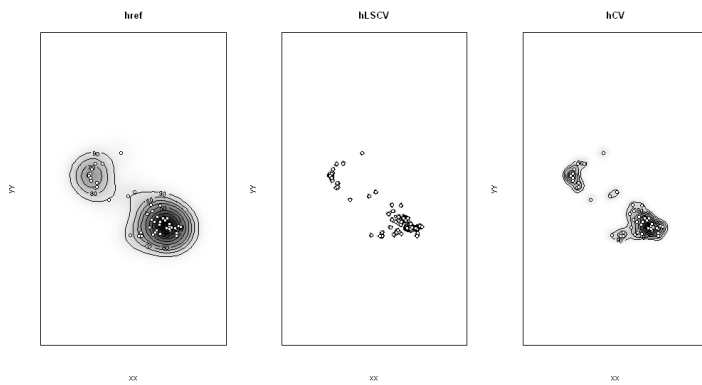
1Paur2009-2-F-A-197 (locs : 34)



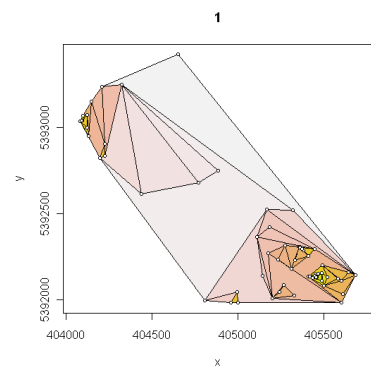
hcv (2CN), DV multimodal : ICP



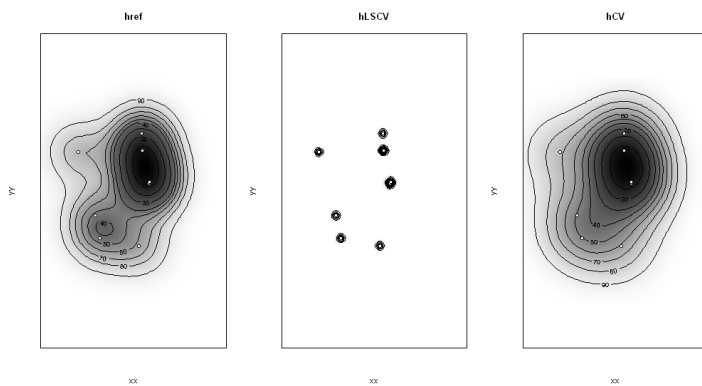
1Paur2009-2-F-A-716 (locs : 92)



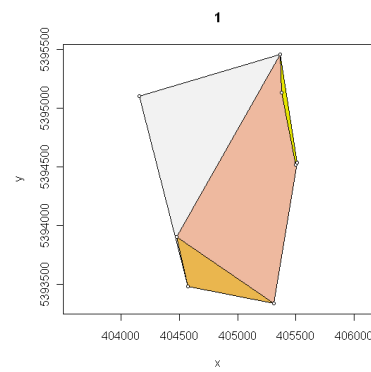
hcv (2BVN), DV multimodal : ICP



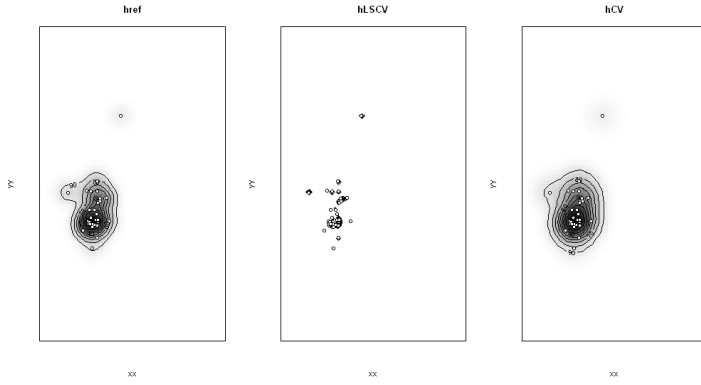
1Paur2009-2-M-A-017 (locs : 10)



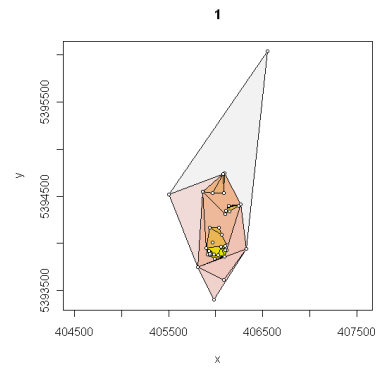
(href) (2BVN), DV multimodal : ICP



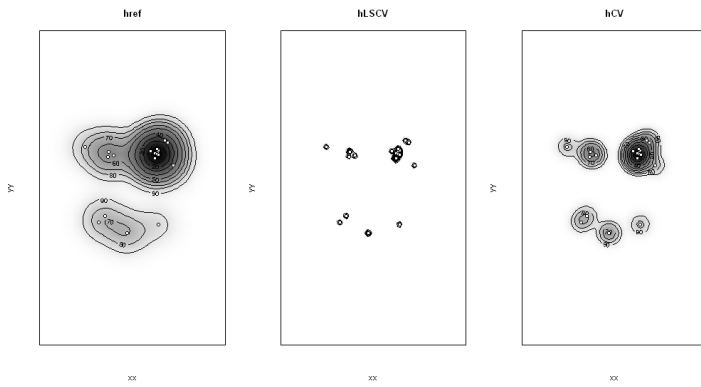
1Paur2009-2-M-A-578 (49)



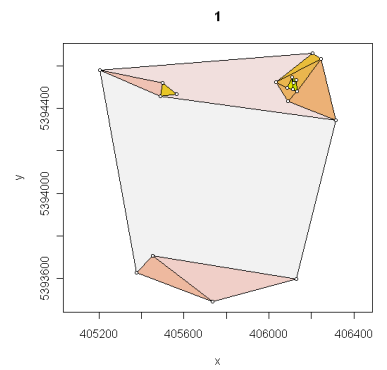
(href) (2BVN), DV multimodal : ICP



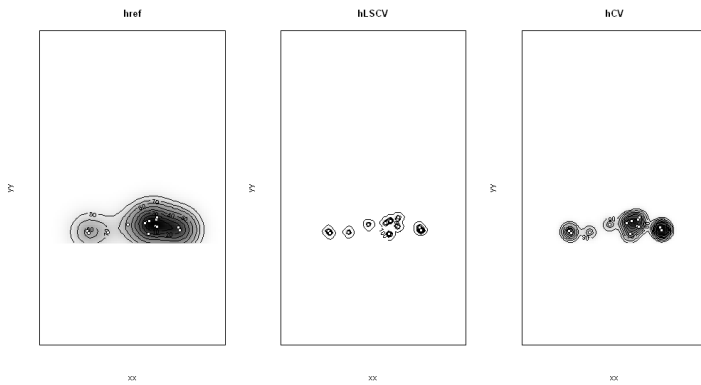
1Paur2009-3-F-A-838 (locs : 30)



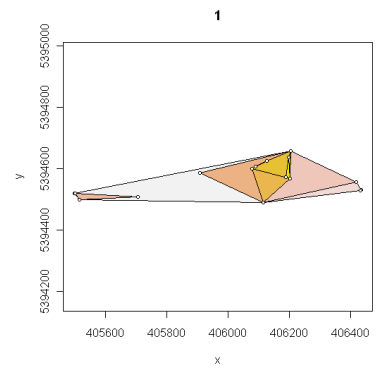
hcv (2BVN), DV multimodal : ICP



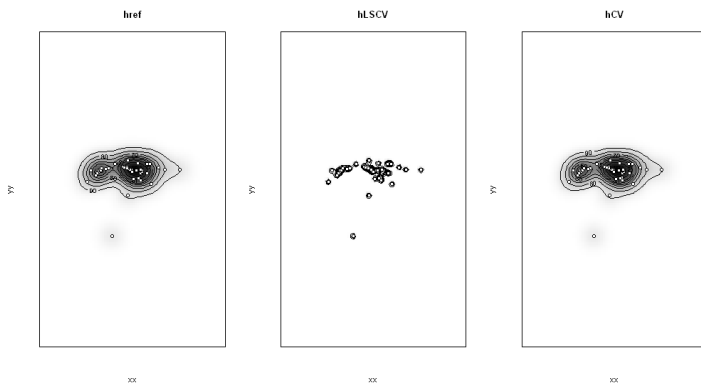
1Paur2009-3-F-J-398 (locs : 22)



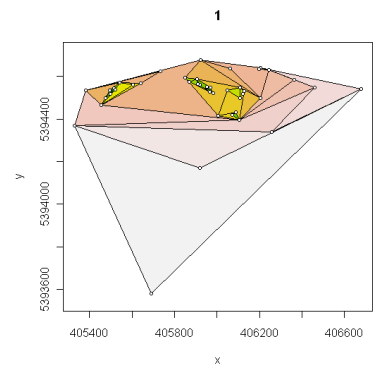
href (BVN), DV bimodal : ICP



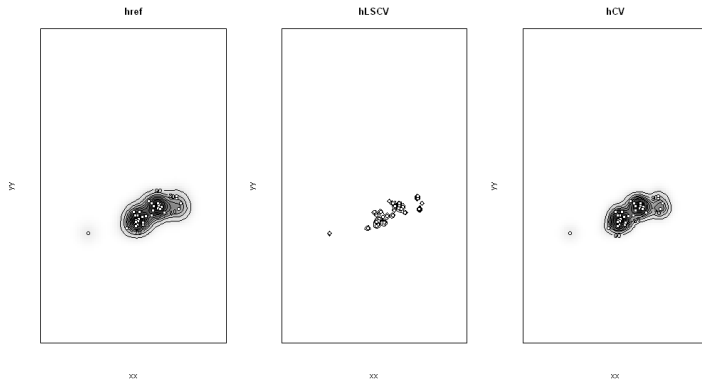
1Paur2009-3-F-PJ-618 (locs : 47)



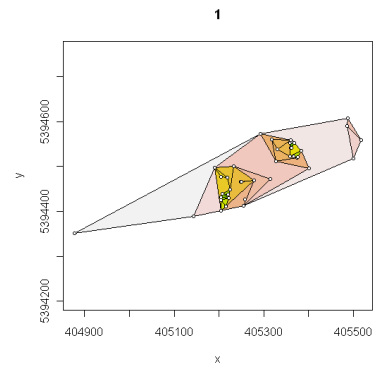
(hcv) (2BVN), DV multimodal : ICP



1Paur2009-3-M-J-798 (locs : 47)



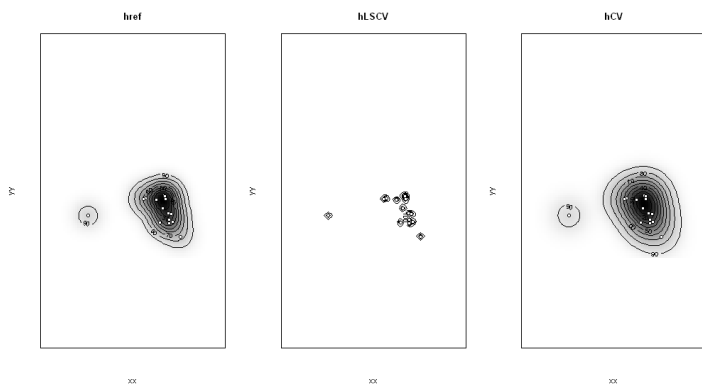
h<sub>CV</sub> (BVN), DV bimodal : ICP



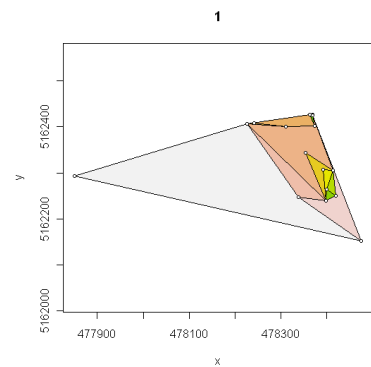
*Plecotus auritus*

Site : Forêt Domaniale de Tronçais

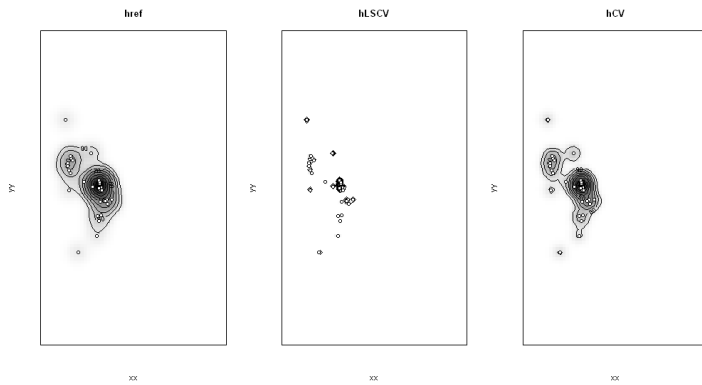
2Paur2006-1-F-A-262 (locs : 18)



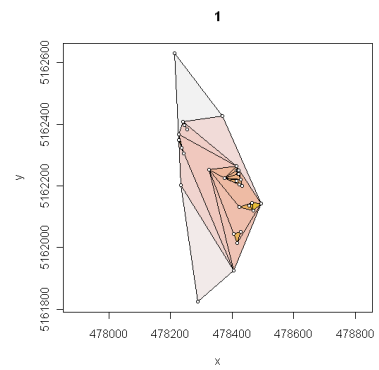
(h<sub>ref</sub>) (2CN), DV multimodal : ICP



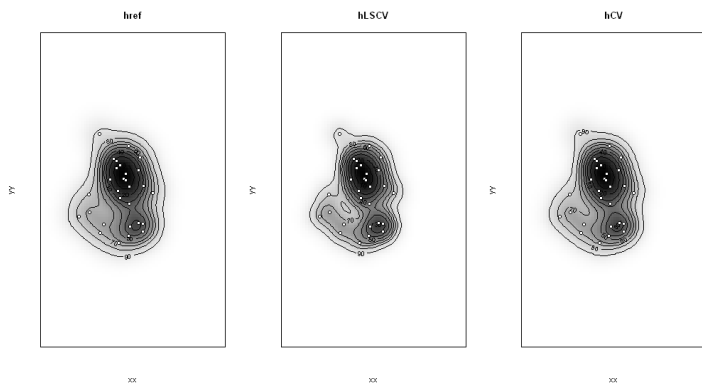
2Paur2006-1-F-A-266 (locs : 69)



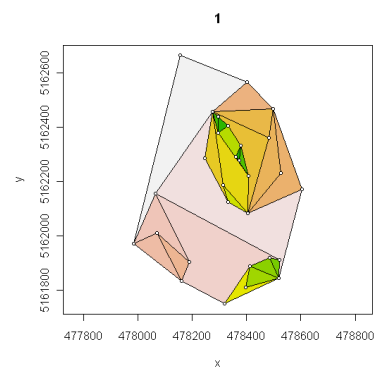
h<sub>CV</sub> (2BVN), DV multimodal : ICP



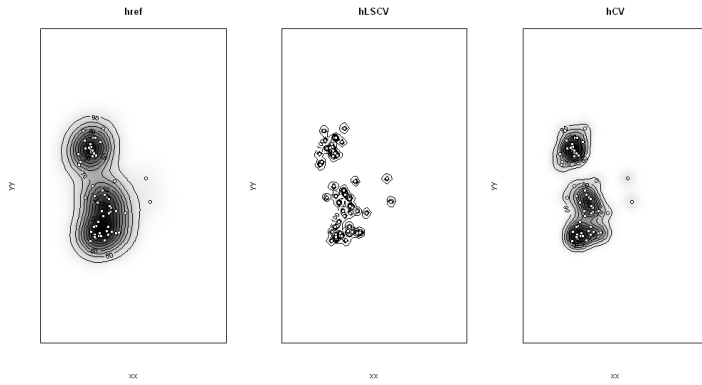
2Paur2007-1-F-A-199 (locs : 32)



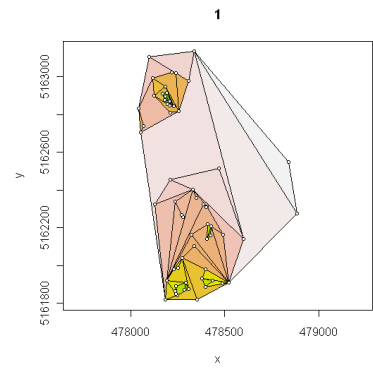
h<sub>LSCV</sub> (BVN), DV bimodal : ICP



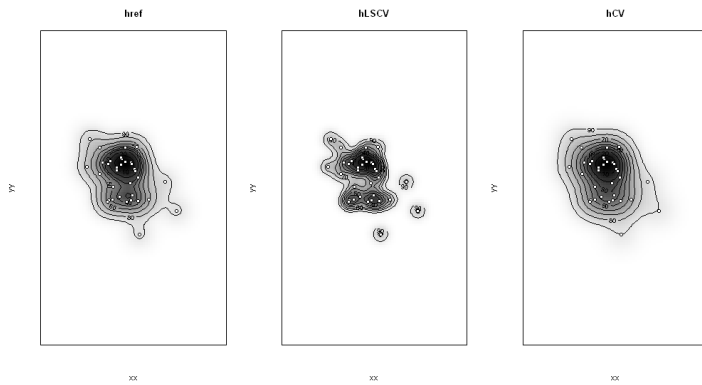
2Paur2007-1-F-A-299 (locs : 74)



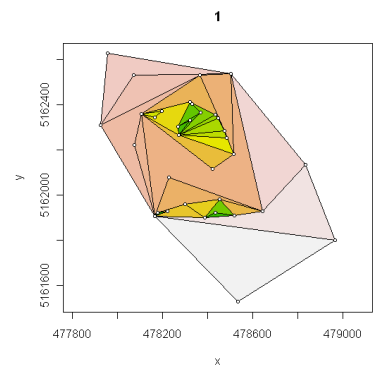
hcv (2BVN), DV multimodal : ICP



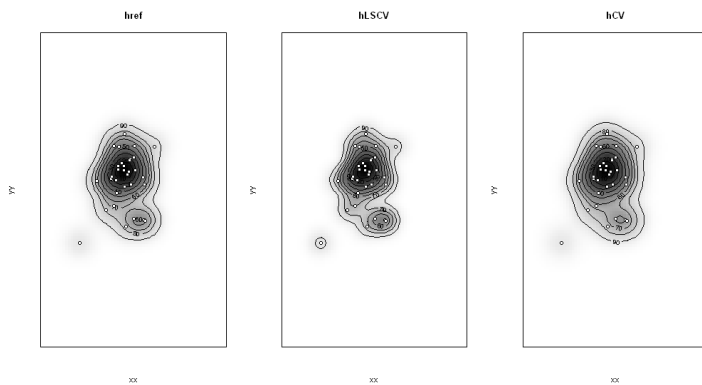
2Paur2007-1-F-A-379 (locs : 38)



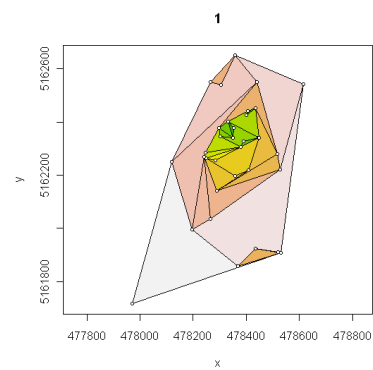
(href-hLscv) (BVN), DV bimodal : ICP



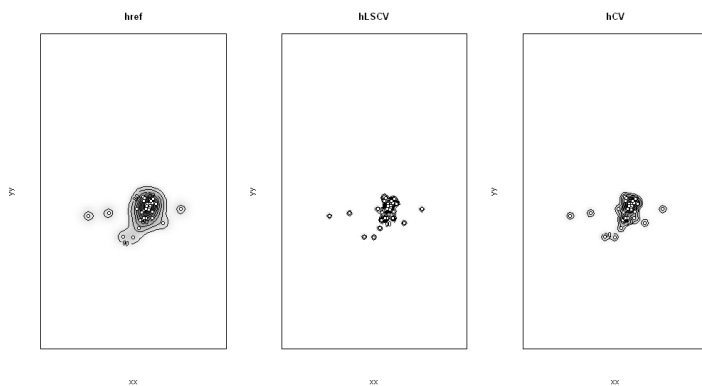
2Paur2007-1-F-A-399 (locs : 38)



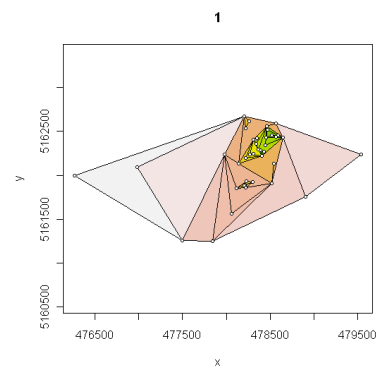
hLscv (2CN), DV multimodal : ICP



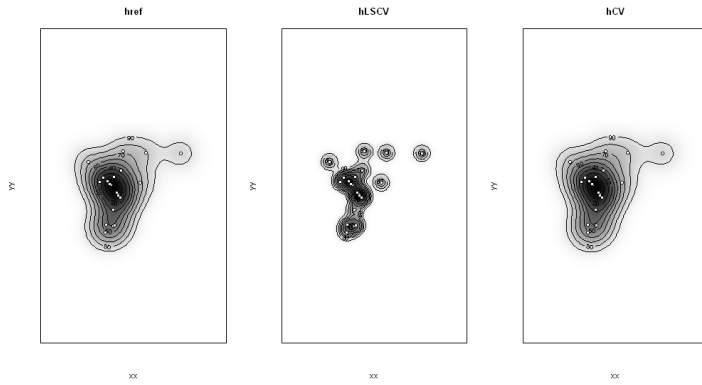
2Paur2007-1-M-A-179 (locs : 44)



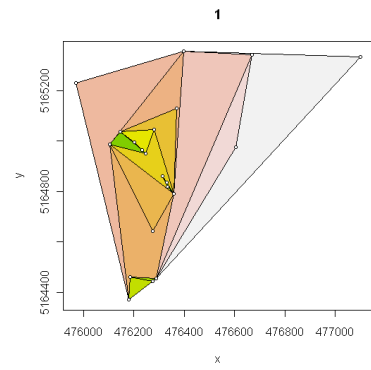
(href-hcv) (2BVN), DV multimodal : ICP



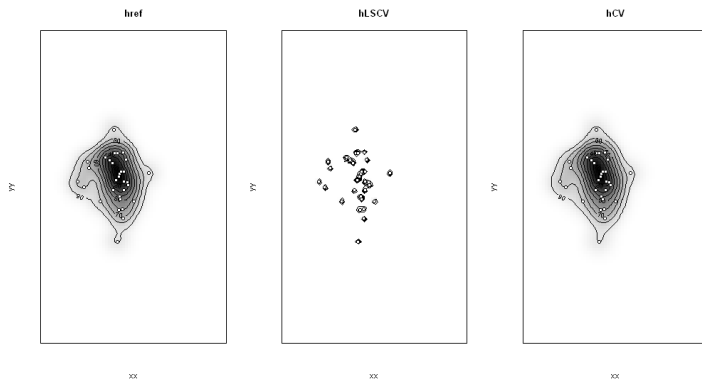
2Pair2007-3-F-A-058 (locs : 22)



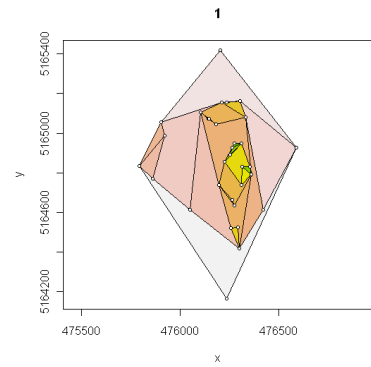
(href) (BVN), DV bimodal : ICP



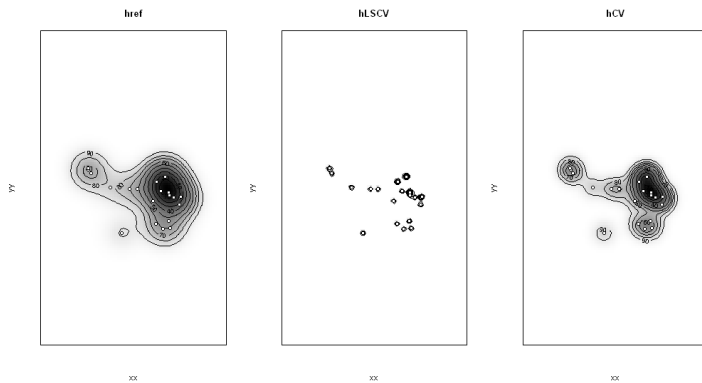
2Pair2007-3-F-A-098 (locs : 41)



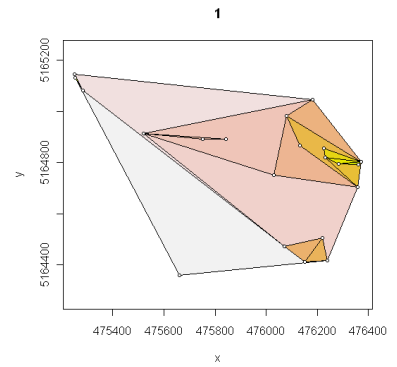
(href) (2BVN), DV multimodal : ICP



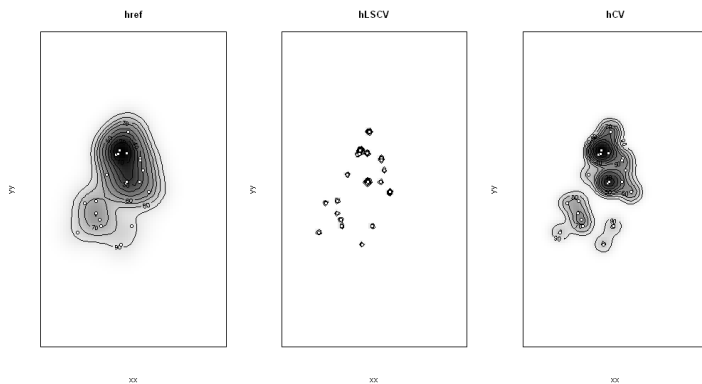
2Pair2007-3-F-A-278 (locs : 33)



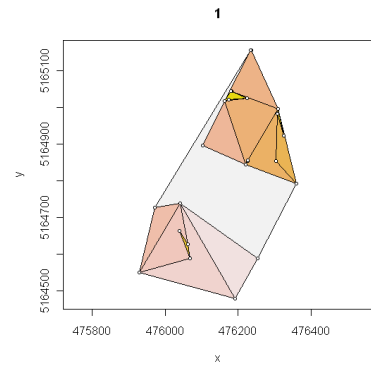
hcv (2CN), DV multimodal : ICP



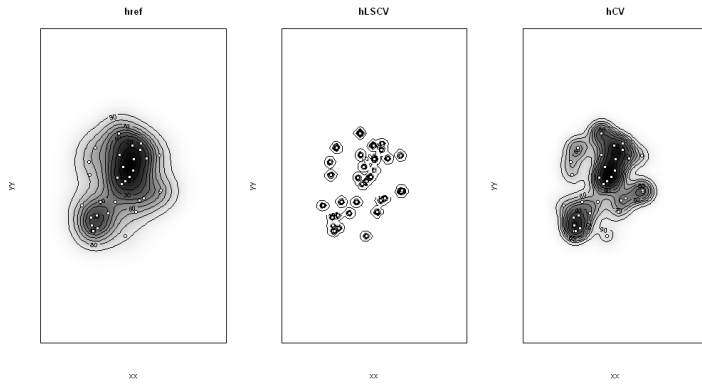
2Pair2007-3-F-A-378 (locs : 37)



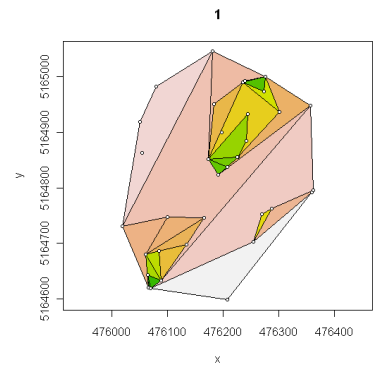
hcv (2BVN), DV multimodal : ICP



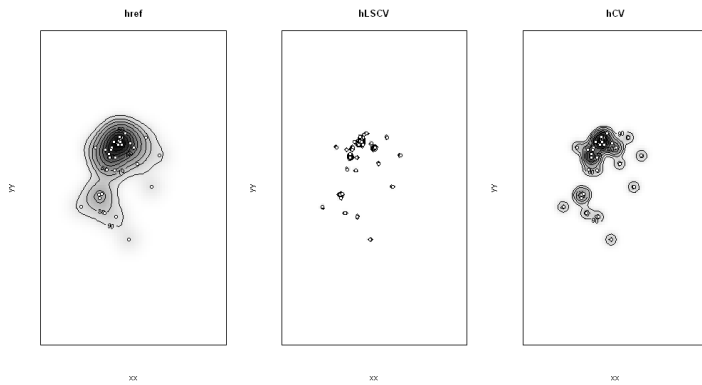
2Paur2007-3-F-A-438 (locs : 41)



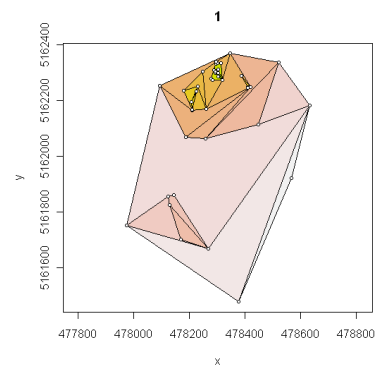
href (CU), DV unimodal : MCP



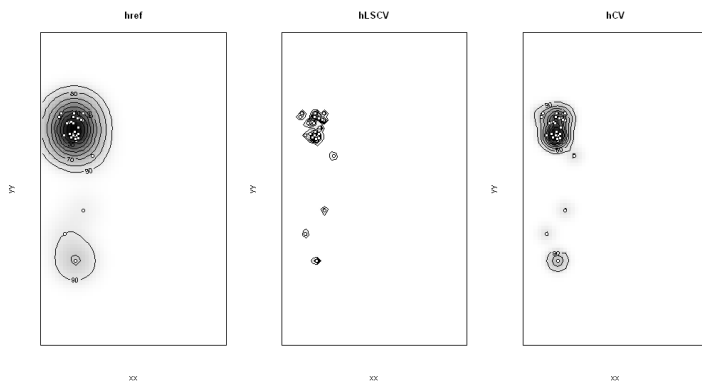
2Paur2008-2-F-A-458 (locs : 53)



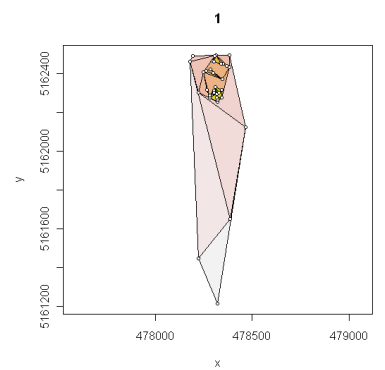
hcv (2BVN), DV multimodal : ICP



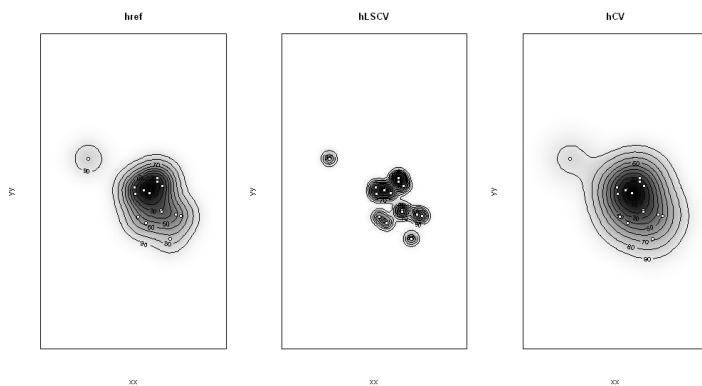
2Paur2008-2-F-A-558 (locs : 53)



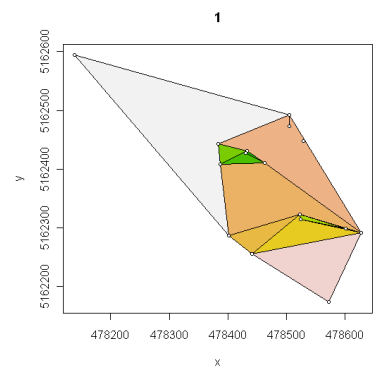
hcv (2BVN), DV multimodal : ICP



2Paur2008-2-F-A-638 (locs : 17)

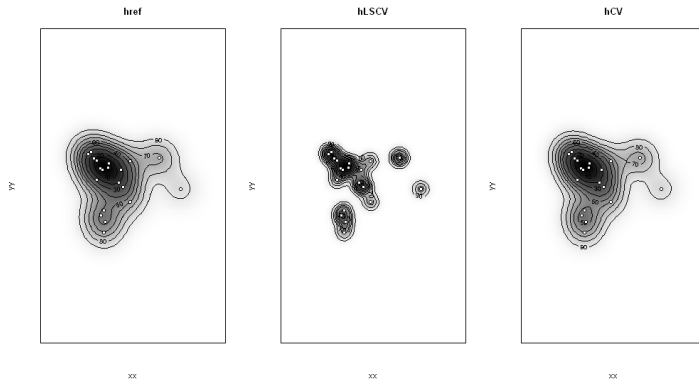


href (BVN), DV bimodal : ICP

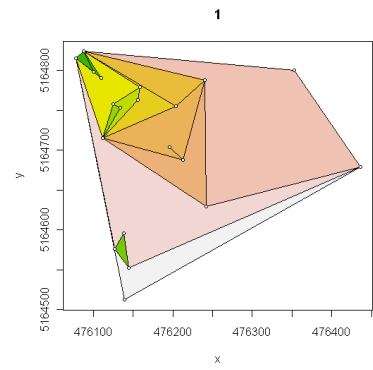




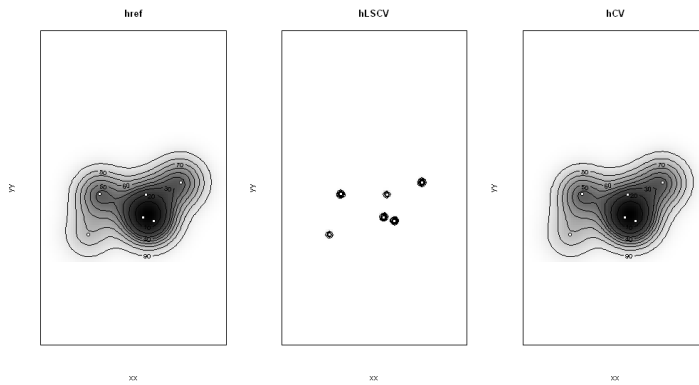
2Paur2008-2-F-A-738 (locs : 23)



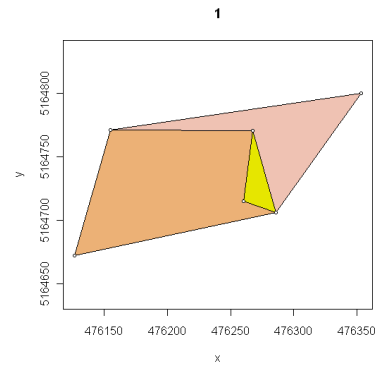
hLscv (2CN), DV multimodal : ICP



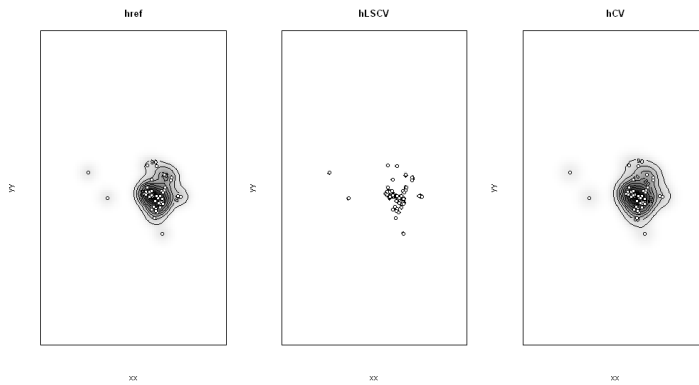
2Paur2008-2-F-A-838 (locs : 10)



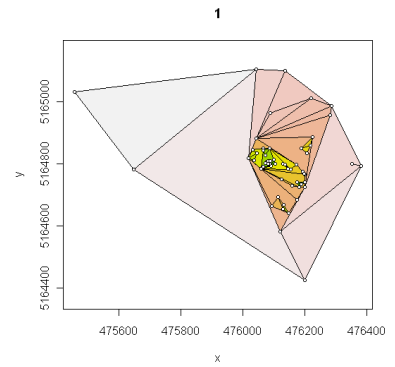
(href-hcv) (2BVN), DV multimodal : ICP



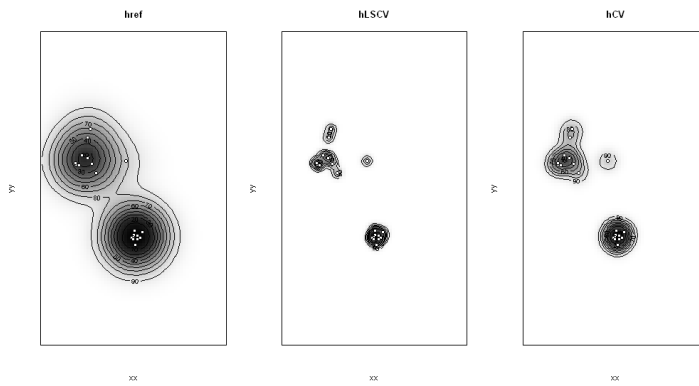
2Paur2008-2-F-A-938 (locs : 62)



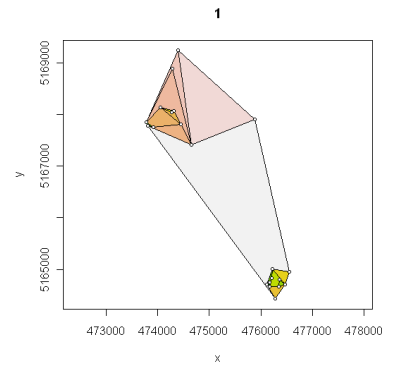
href (2BVN), DV multimodal : ICP



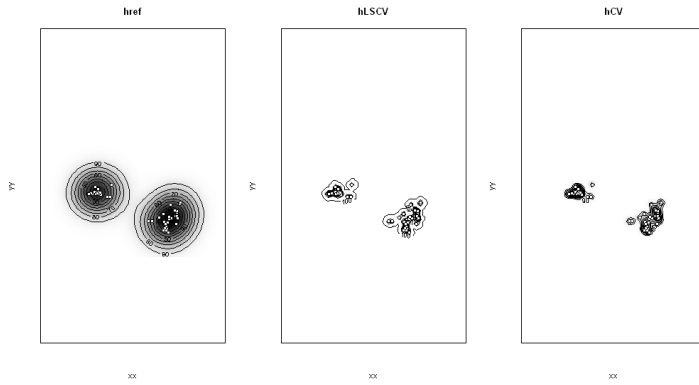
2Paur2008-2-M-PJ-638 (locs : 23)



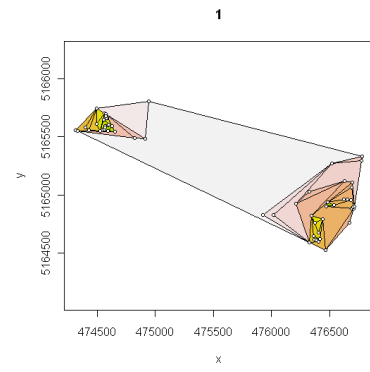
hLscv (2CN), DV multimodal : ICP



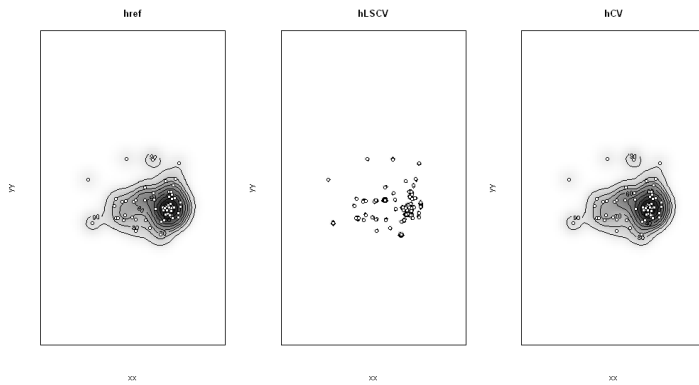
2Paur2008-3-F-A-537 (locs : 62)



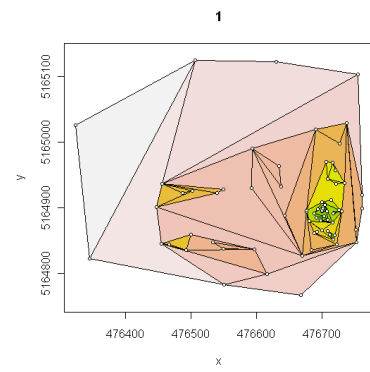
hcv (2BVN), DV multimodal : ICP



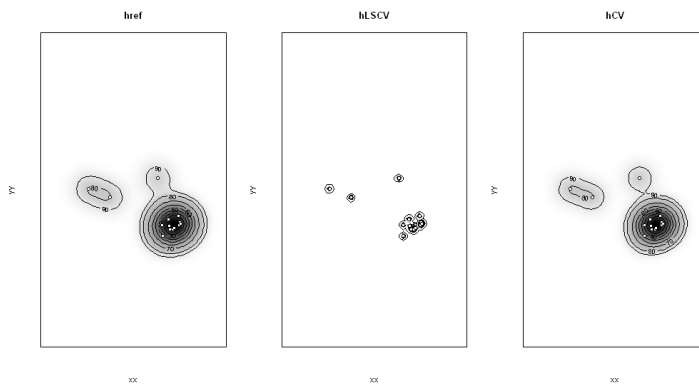
2Paur2008-3-F-A-577 (locs : 91)



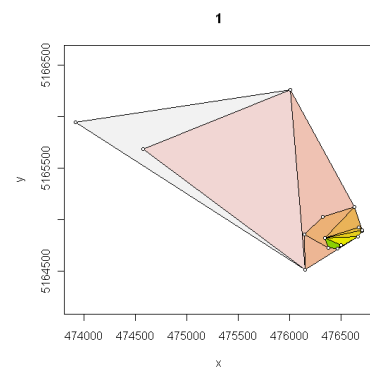
hcv-href (2CN), DV multimodal : ICP



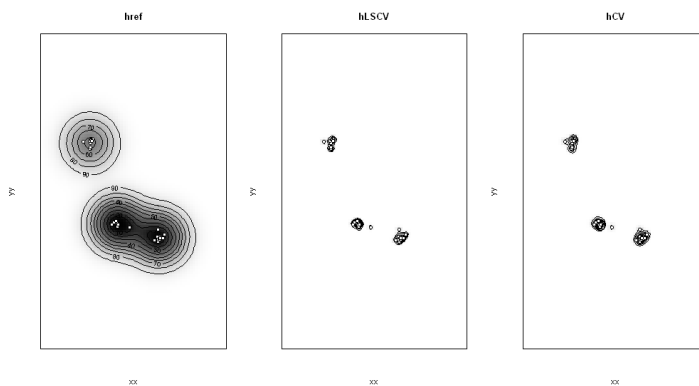
2Paur2008-3-F-A-657 (locs : 20)



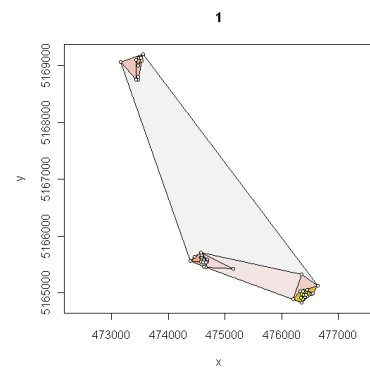
hcv (2CN), DV multimodal : ICP



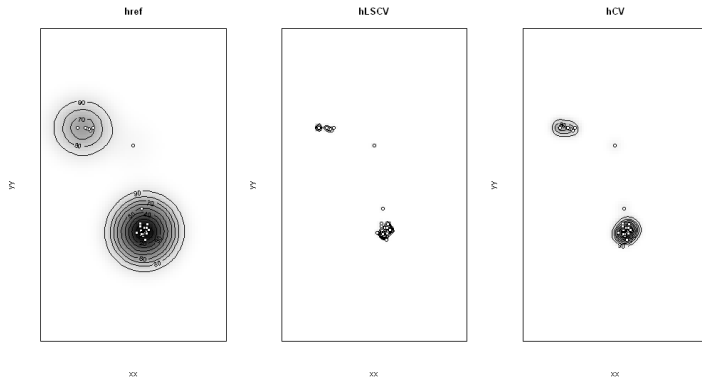
2Paur2008-3-F-A-797 (locs : 47)



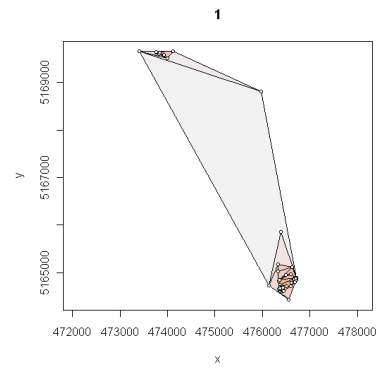
hcv (2BVN), DV multimodal : ICP



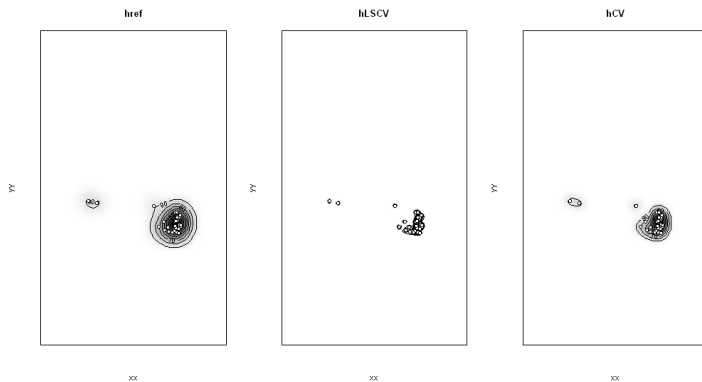
2Pair2008-3-F-A-977 (locs : 75)



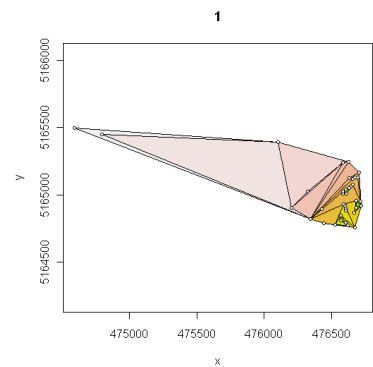
h<sub>CV</sub> (2BVN), DV multimodal : ICP



2Pair2008-3-M-A-697 (locs : 40)



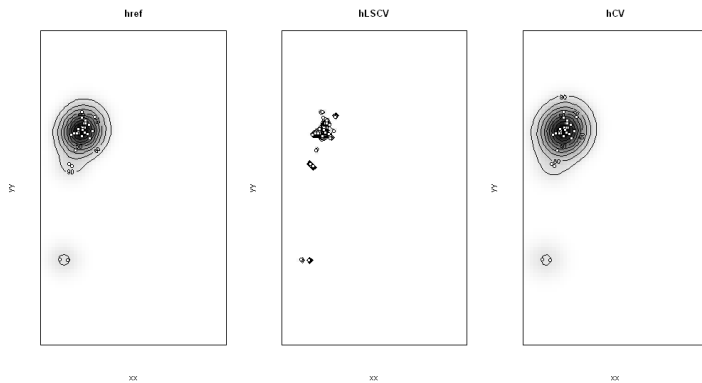
h<sub>CV</sub> (2BVN), DV multimodal : ICP



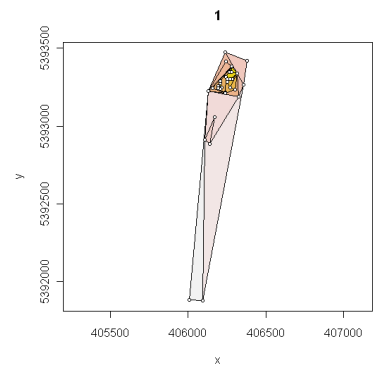
*Pipistrellus pipistrellus*

Site : Forêt Domaniale de Rambouillet

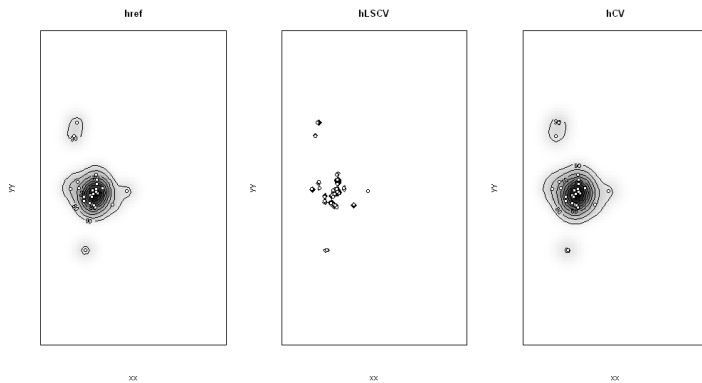
1Ppi2007-1-M-A-019 (locs : 43)



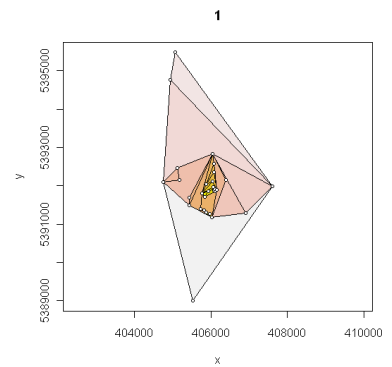
h<sub>ref</sub> (2BVN), DV multimodal : ICP



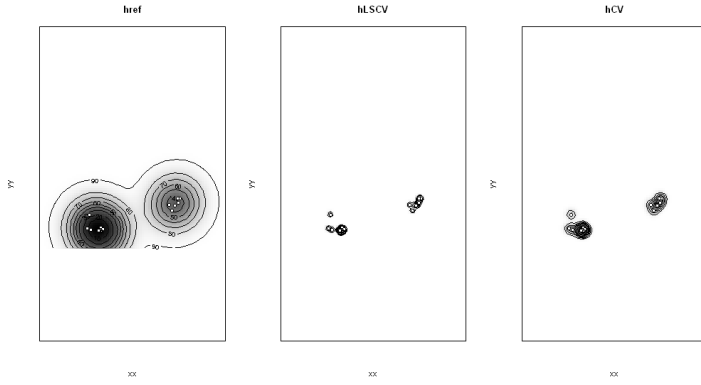
1Ppi2007-1-M-A-219 (locs : 42)



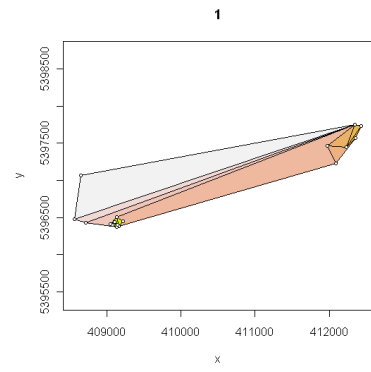
h<sub>ref</sub> (2BVN), DV multimodal : ICP



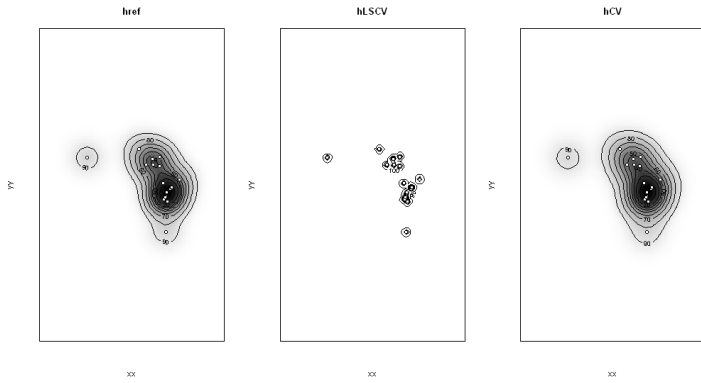
1Ppi2007-2-F-A-278 (locs : 21)



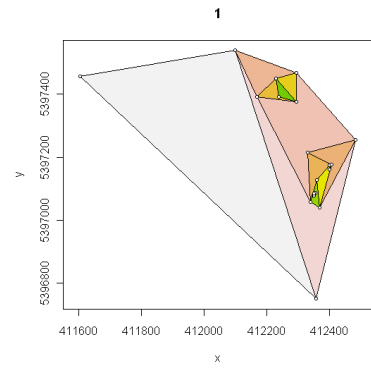
hcv (2CN), DV multimodal : ICP



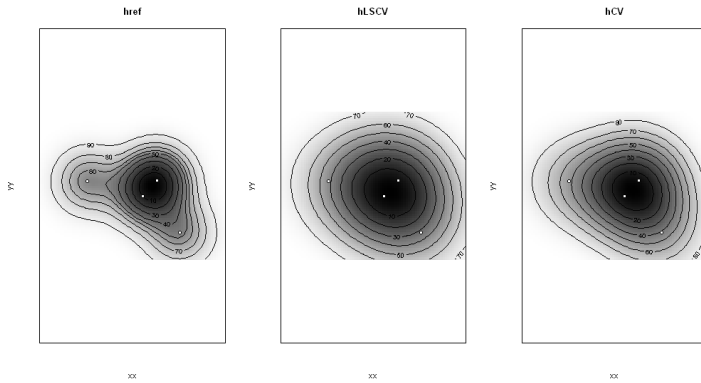
1Ppi2007-2-M-A-100 (locs : 21)



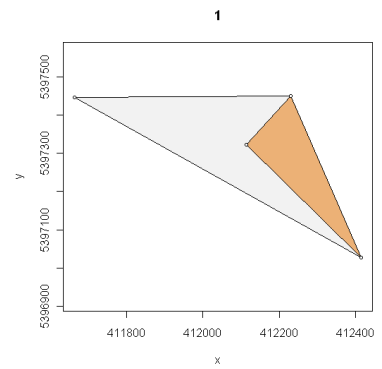
(href) (2CN), DV multimodal : ICP



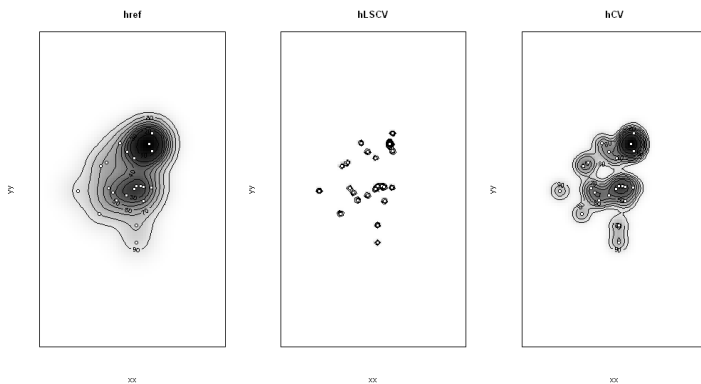
1Ppi2007-2-M-A-258 (locs : 5)



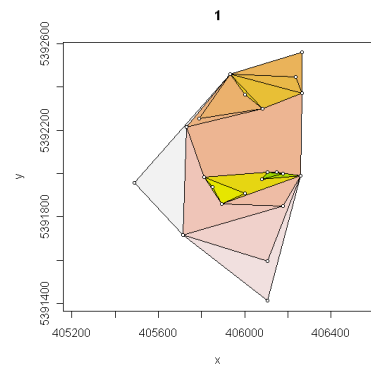
(href) (2BVN), DV multimodal : ICP



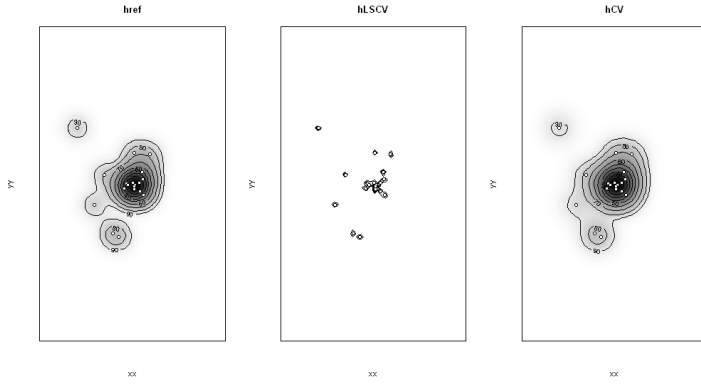
1Ppi2007-3-F-A-419 (locs : 30)



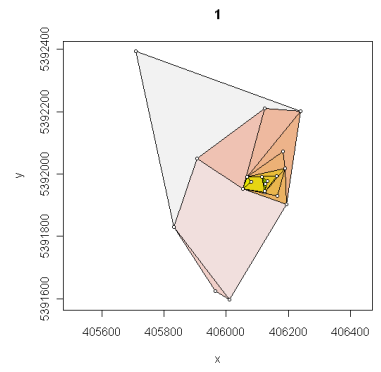
hcv (2BVN), DV multimodal : ICP



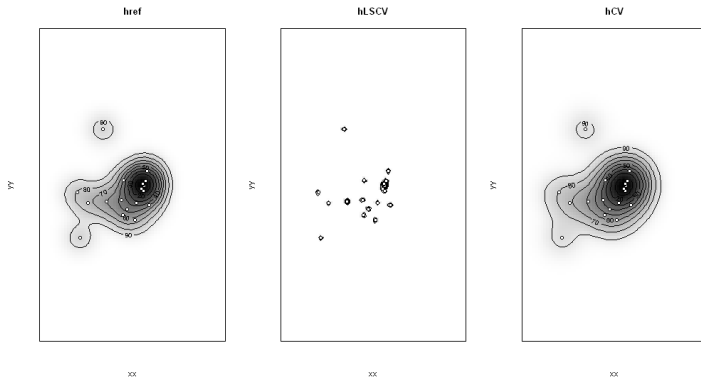
1Ppi2007-3-M-A-319 (locs : 29)



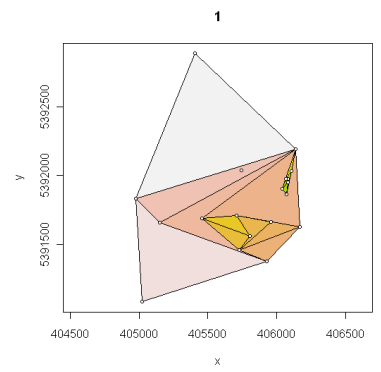
href (2CN), DV multimodal : ICP



1Ppi2007-3-M-A-359 (locs : 27)



href (2CN), DV multimodal : ICP



**Annexe 2 (Chapitre 6) : Résultats des modélisations obtenues à l'aide du logiciel Animal Space Use 1,3 Beta, présentant pour chaque individu les différents modèles observés** ayant une valeur d'AICc proche. Est retenu le modèle ayant le plus faible AICc (en premier pour chaque individu). ID : identifiant de l'individu (« 1Ppi2007-2-M-A-258 »=forêt (1 :Rambouillet, 2 :Tronçais), Espèce, Année-période2-Mâle-Adulte-code de l'émetteur) ; Loci : nombre de localisations obtenues par télémétrie pour l'animal ; M : Modèle obtenu ; NP : nombre de paramètres retenus pour calculer chaque modèle ; AICc : valeur de l'AICc obtenu pour chaque modèle ; Forme : forme du modèle (unimodal (CU), bimodal (BVN) ou multimodal (2CN ou 2BVN)).

ID	Loc	M	NP	AICc	Forme	ID	Loc	M	NP	AICc	Shape
<b><i>Myotis bechsteinii</i></b>											
1Mbe2006-2-F-A-558	20	2BVN	11	298.857	Multimodal	1Mbe2007-3-F-J-337	54	2BVN	11	1404.65	Multimodal
1Mbe2009-3-F-J-638	31	2BVN	11	875.924	Multimodal	2Mbe2006-3-F-A-901.2	54	2BVN	11	947.468	Multimodal
		2CN	7	879.149	Multimodal	1Mbe2006-3-F-A-958	55	2CN	7	1307.86	Multimodal
2Mbe2008-3-F-J-918	31	2CN	7	807.376	Multimodal	1Mbe2006-2-F-A-778.2	56	2BVN	11	1311.61	Multimodal
		CU	4	810.362	Unimodal			2CN	7	1317.98	Multimodal
		BVN	6	810.96	Bimodal	1Mbe2007-3-F-A-118	56	2BVN	11	1385.71	Multimodal
		2BVN	11	823.19	Multimodal	2Mbe2008-3-F-A-818	56	2BVN	11	1289.76	Multimodal
2Mbe2008-2-F-PJ-498	32	2CN	7	788.907	Multimodal			2CN	7	1303.06	Multimodal
		2BVN	11	809.54	Multimodal	1Mbe2006-3-M-J-597	57	2BVN	11	1319.38	Multimodal
2Mbe2008-2-M-A-838	32	2CN	7	756.243	Multimodal	2Mbe2008-2-F-A-478	58	2BVN	11	1398.39	Multimodal
2Mbe2006-2-F-A-272	33	2BVN	11	747.355	Multimodal			2CN	7	1399.56	Multimodal
		2CN	7	748.58	Multimodal	2Mbe2006-3-F-A-901	59	2BVN	11	1263.91	Multimodal
1Mbe2006-2-M-A-898.1	35	2CN	7	789.792	Multimodal	1Mbe2009-3-F-J-558	60	2BVN	11	1435.79	Multimodal
2Mbe2008-3-F-A-898	35	BVN	6	844.252	Bimodal	2Mbe2008-3-M-J-718	60	2BVN	11	1305.35	Multimodal
		2CN	7	847.815	Multimodal			2CN	7	1314.82	Multimodal
		CU	4	849.203	Unimodal	2Mbe2006-3-F-A-748	62	2BVN	11	1289.34	Multimodal
		2BVN	11	859.136	Multimodal			BVN	6	1297.03	Bimodal
2Mbe2006-1-F-A-263-2	38	2CN	7	797.175	Multimodal			2CN	7	1299.72	Multimodal
		2BVN	11	805.951	Multimodal			CU	4	1302.8	Unimodal
1Mbe2009-2-M-A-598	39	BVN	6	973.543	Bimodal	1Mbe2009-3-F-A-478	69	2CN	7	2073.39	Multimodal
		2BVN	11	976.399	Multimodal			2BVN	11	2073.5	Multimodal
2Mbe2006-2-F-A-274	39	2BVN	11	988.123	Multimodal	1Mbe2009-3-F-A-338	70	2BVN	11	1687.03	Multimodal
		2CN	7	999.002	Multimodal			2CN	7	1706.54	Multimodal
2Mbe2007-3-M-A-178	40	2CN	7	918.054	Multimodal	2Mbe2008-2-F-A-438	73	2BVN	11	1712.4	Multimodal
		2BVN	11	920.754	Multimodal			2CN	7	1718.73	Multimodal
1Mbe2006-2-F-A-578	42	2CN	7	901.095	Multimodal	2Mbe2008-3-F-A-858	73	2BVN	11	1673.94	Multimodal
2Mbe2008-2-F-A-738	43	2CN	7	1016.279	Multimodal	2Mbe2008-3-F-A-778	76	2BVN	11	1716.11	Multimodal
		2BVN	11	1023.418	Multimodal			2CN	7	1716.67	Multimodal
1Mbe2007-3-F-A-138	44	2CN	7	1261.186	Multimodal	2Mbe2008-3-F-J-758	79	2BVN	11	2044.78	Multimodal
		2BVN	11	1268.46	Multimodal			2CN	7	2070.45	Multimodal
1Mbe2009-3-F-A-738	46	2BVN	11	1253.451	Multimodal	2Mbe2008-3-F-A-618	90	2BVN	11	2104.77	Multimodal
		2CN	7	1257.98	Multimodal			2CN	7	2112.06	Multimodal
1Mbe2007-3-F-A-158	47	2CN	7	1283.321	Multimodal	1Mbe2006-1-M-A-478	105	2CN	7	2439.17	Multimodal
2Mbe2008-2-F-A-518	48	2BVN	11	1182.327	Multimodal			2BVN	11	2444.16	Multimodal
		2CN	7	1197.61	Multimodal	1Mbe2006-3-F-A-917	116	2CN	7	3181.32	Multimodal
1Mbe2006-2-F-A-738	49	2BVN	11	1310.516	Multimodal	1Mbe2006-3-F-J-940	120	2BVN	11	3058.25	Multimodal
1Mbe2009-3-F-J-978	51	2CN	7	1453.226	Multimodal	1Mbe2006-3-F-A-977	149	2BVN	11	3773.06	Multimodal
		2BVN	11	1454.48	Multimodal			2CN	7	3788.48	Multimodal
2Mbe2006-3-F-A-748.2	51	2CN	7	1063.804	Multimodal			2BVN	11	1072.87	Multimodal
		2BVN	11	1072.87	Multimodal						
<b><i>Myotis nattereri</i></b>											
1Mna2009-3-F-J-497	12	2BVN	11	68.693	Multimodal	1Mna2009-2-F-A-179	38	2CN	7	1032.1	Multimodal
1Mna2009-2-F-A-398	23	2CN	7	640.472	Multimodal			2BVN	11	1032.33	Multimodal
1Mna2009-3-F-J-898	23	2CN	7	545.102	Multimodal	1Mna2009-3-F-A-697	40	2BVN	11	883.023	Multimodal
1Mna2009-3-F-J-677	25	2CN	7	622.992	Multimodal			2CN	7	907.589	Multimodal

		BVN	6	634.31	Bimodal	1Mna2009-2-F-A-139	43	2CN	7	1116.71	Multimodal
		CU	4	639.694	Unimodal			2BVN	11	1116.91	Multimodal
		2BVN	11	640.796	Multimodal	1Mna2009-3-F-J-418	44	2BVN	11	1098.58	Multimodal
1Mna2009-2-F-A-158	29	2CN	7	715.465	Multimodal			2CN	7	1110.38	Multimodal
		2BVN	11	734.356	Multimodal	1Mna2009-3-F-J-599	48	2BVN	11	1364.21	Multimodal
1Mna2009-2-F-A-219	29	2BVN	11	918.844	Multimodal	1Mna2009-3-F-J-458	56	CU	4	1399.49	Unimodal
		2CN	7	921.729	Multimodal	1Mna2009-3-F-A-858	59	2CN	7	1364.47	Multimodal
1Mna2009-3-F-J-658	31	2BVN	11	822.254	Multimodal	1Mna2009-2-F-A-119	63	2BVN	11	1456.98	Multimodal
		2CN	7	823.183	Multimodal	1Mna2009-3-F-J-918	66	2BVN	11	1599.48	Multimodal
		CU	4	836.765	Unimodal	1Mna2009-2-F-A-238	76	2BVN	11	1606.87	Multimodal
		BVN	6	837.214	Bimodal			2CN	7	1631.65	Multimodal

### ***Plecotus auritus***

1Paur2006-2-F-A-798	5	2BVN	11	59.577	Multimodal	1Paur2009-2-F-A-058	35	2BVN	11	886.405	Multimodal
1Paur2006-1-F-A-419	8	2CN	7	99.29	Multimodal	2Paur2007-3-F-A-378	37	2BVN	11	903.914	Multimodal
1Paur2009-2-M-A-017	10	2BVN	11	206.317	Multimodal			2CN	7	906.437	Multimodal
2Paur2008-2-F-A-838	10	2BVN	11	101.157	Multimodal			BVN	6	908.551	Bimodal
1Paur2006-1-F-A-458	11	2BVN	11	178.888	Multimodal	2Paur2007-1-F-A-379	38	BVN	6	1017.78	Bimodal
1Paur2009-2-F-A-077	11	2BVN	11	144.933	Multimodal			2CN	7	1020	Multimodal
1Paur2006-1-F-A-179	12	2BVN	11	-36.522	Multimodal			CU	4	1022.16	Unimodal
1Paur2006-2-F-A-498	16	2CN	7	423.016	Multimodal			2BVN	11	1024.71	Multimodal
2Paur2008-2-F-A-638	17	BVN	6	400.125	Bimodal	2Paur2007-1-F-A-399	38	2CN	7	967.608	Multimodal
		CU	4	402.071	Unimodal			BVN	6	970.784	Bimodal
		2CN	7	411.139	Multimodal	1Paur2009-1-F-A-696	40	BVN	6	1040.49	Bimodal
1Paur2006-3-F-A-858	18	2CN	7	424.636	Multimodal			2BVN	11	1040.82	Multimodal
		CU	4	432.158	Unimodal	2Paur2008-3-M-A-697	40	2BVN	11	1023.45	Multimodal
		BVN	6	434.223	Bimodal			2CN	7	1028.36	Multimodal
2Paur2006-1-F-A-262	18	2CN	7	397.777	Multimodal	2Paur2007-3-F-A-098	41	2BVN	11	1068.44	Multimodal
1Paur2006-1-M-A-138	19	2CN	7	404.767	Multimodal			BVN	6	1072.22	Bimodal
		BVN	6	429.88	Bimodal			2CN	7	1078.18	Multimodal
1Paur2006-2-M-A-198	20	2CN	7	492.626	Multimodal			CU	4	1079.31	Unimodal
		BVN	6	508.469	Bimodal	2Paur2007-3-F-A-438	41	CU	4	976.567	Unimodal
		CU	4	511.777	Unimodal			2CN	7	984.998	Multimodal
1Paur2009-1-M-A-857	20	BVN	6	433.961	Bimodal			BVN	6	986.181	Bimodal
		CU	4	438.355	Unimodal	1Paur2009-1-F-A-897	43	2CN	7	936.798	Multimodal
		2CN	7	438.589	Multimodal			2BVN	11	940.267	Multimodal
2Paur2008-3-F-A-657	20	2CN	7	571.791	Multimodal	2Paur2007-1-M-A-179	44	2BVN	11	1236.16	Multimodal
		2BVN	11	581.731	Multimodal			2CN	7	1240.14	Multimodal
1Paur2006-2-F-A-838	22	2CN	7	530.802	Multimodal	1Paur2009-1-F-A-355	46	2BVN	11	1042.96	Multimodal
1Paur2006-2-M-A-898.2	22	BVN	6	551.815	Bimodal			2CN	7	1053.95	Multimodal
		2CN	7	556.214	Multimodal			BVN	6	1059.29	Bimodal
1Paur2009-3-F-J-398	22	BVN	6	533.582	Bimodal	1Paur2006-3-M-A-877	47	2CN	7	1032.37	Multimodal
		2BVN	11	545.585	Multimodal			BVN	6	1035.05	Bimodal
2Paur2007-3-F-A-058	22	BVN	6	596.049	Bimodal			2BVN	11	1035.91	Multimodal
		CU	4	597.362	Unimodal	1Paur2009-3-F-PJ-618	47	2BVN	11	1243.16	Multimodal
		2CN	7	603.508	Multimodal			2CN	7	1248.69	Multimodal
		2BVN	11	610.722	Multimodal	1Paur2009-3-M-J-798	47	BVN	6	1042.93	Bimodal
2Paur2008-2-F-A-738	23	2CN	7	524.645	Multimodal			2BVN	11	1049.23	Multimodal
		CU	4	527.394	Unimodal	2Paur2008-3-F-A-797	47	2BVN	11	1353.75	Multimodal
		BVN	6	530.632	Bimodal	1Paur2009-2-F-A-038	48	2BVN	11	1146.73	Multimodal
		2BVN	11	539.049	Multimodal			2CN	7	1162.09	Multimodal
2Paur2008-2-M-PJ-638	23	2CN	7	673.245	Multimodal	1Paur2009-1-M-A-037	49	2BVN	11	1149.63	Multimodal
1Paur2006-1-M-A-118	24	2CN	7	612.985	Multimodal			CU	4	1162.45	Unimodal
		CU	4	618.939	Unimodal	1Paur2009-2-M-A-578	49	2BVN	11	1311.44	Multimodal
		BVN	6	621.095	Bimodal	1Paur2007-2-F-A-118	52	2BVN	11	1293.62	Multimodal
1Paur2007-2-M-A-100	24	BVN	6	637.294	Bimodal			2CN	7	1298.83	Multimodal
		CU	4	640.488	Unimodal	2Paur2008-2-F-A-458	53	2BVN	11	1278.95	Multimodal
		2BVN	11	641.387	Multimodal			2CN	7	1296.73	Multimodal
		2CN	7	641.737	Multimodal	2Paur2008-2-F-A-558	53	2BVN	11	1257.15	Multimodal
1Paur2007-1-F-A-058	25	2BVN	11	632.769	Multimodal			2CN	7	1268.09	Multimodal
		2CN	7	659.034	Multimodal	1Paur2006-1-F-A-438	61	2BVN	11	1656.52	Multimodal

1Paur2009-1-F-A-096	27	2CN	7	653.792	Multimodal			2CN	7	1659.88	Multimodal
1Paur2009-1-F-A-977	27	2BVN	11	659.132	Multimodal			BVN	6	1665.66	Bimodal
1Paur2009-3-F-A-838	30	2BVN	11	765.95	Multimodal	2Paur2008-2-F-A-938	62	2BVN	11	1497.88	Multimodal
		2CN	7	775.679	Multimodal			2CN	7	1499.38	Multimodal
1Paur2006-3-M-J-537	32	2CN	7	957.415	Multimodal	2Paur2008-3-F-A-537	62	2BVN	11	1674.83	Multimodal
		BVN	6	967.458	Bimodal			2CN	7	1686.72	Multimodal
		2BVN	11	972.82	Multimodal	1Paur2007-1-F-A-078	65	2CN	7	1850	Multimodal
		CU	4	977.728	Unimodal			2BVN	11	1853.6	Multimodal
2Paur2007-1-F-A-199	32	BVN	6	836.401	Bimodal	1Paur2009-1-F-A-055	68	2BVN	11	1669.08	Multimodal
		2CN	7	836.667	Multimodal			2CN	7	1678.78	Multimodal
		CU	4	839.177	Unimodal	2Paur2006-1-F-A-266	69	2BVN	11	1411.67	Multimodal
		2BVN	11	846.375	Multimodal	2Paur2007-1-F-A-299	74	2BVN	11	1960.87	Multimodal
1Paur2006-1-M-A-278	33	2CN	7	834.908	Multimodal			2CN	7	1971.43	Multimodal
		2BVN	11	838.085	Multimodal	2Paur2008-3-F-A-977	75	2BVN	11	2238.2	Multimodal
2Paur2007-3-F-A-278	33	2CN	7	885.061	Multimodal	2Paur2008-3-F-A-577	91	2CN	7	2017.66	Multimodal
		2BVN	11	886.245	Multimodal			2BVN	11	2019.26	Multimodal
1Paur2009-2-F-A-197	34	2CN	7	832.996	Multimodal	1Paur2009-2-F-A-716	92	2BVN	11	2470.72	Multimodal
		2BVN	11	835.375	Multimodal			2CN	7	2474.18	Multimodal
<b><i>Pipistrellus pipistrellus</i></b>						1Ppi2007-3-M-A-359	27	2CN	7	561.473	Multimodal
1Ppi2007-2-M-A-258	5	2BVN	11	75.067	Multimodal	1Ppi2007-3-M-A-319	29	2CN	7	661.334	Multimodal
		CU	4	75.845	Unimodal	1Ppi2007-3-F-A-419	30	2BVN	11	771.993	Multimodal
1Ppi2007-2-F-A-278	21	2CN	7	576.861	Multimodal			2CN	7	783.426	Multimodal
		2BVN	11	595.228	Multimodal	1Ppi2007-1-M-A-219	42	2BVN	11	1246.01	Multimodal
1Ppi2007-2-M-A-100	21	2CN	7	523.102	Multimodal			2CN	7	1260.56	Multimodal
		BVN	6	538.254	Bimodal	1Ppi2007-1-M-A-019	43	2BVN	11	996.78	Multimodal



**Annexe 3 (Chapitre 6) : Modèles observés et facteurs de lissage obtenus pour les 3 méthodes de calcul.** Dans le cas de  $h_{LSCV}$ , la plupart des calculs ne convergent pas (nc), et ne permettent pas de produire des surfaces de DV à partir de cette méthode.

ID	ASU- h <sub>ref</sub>	R-h <sub>ref</sub>	Modèle observé	h <sub>ref</sub> 95	ASU- h <sub>iscv</sub>	R-h <sub>iscv</sub>	Modèle observé	h <sub>iscv</sub> 95	ASU- h <sub>cv</sub>	Modèle observé	h <sub>cv</sub> 95	Modèle valide/ retenu	Home Range Method
1Mbe2006-1-M-A-478	76.75	76.3	Bi	49.85	0.239	nc	-	-	42.97	Multi	30.84	h <sub>cv</sub>	Multimodal
1Mbe2006-2-F-A-558	89.11	86.01	Multi	60.55	0.131	nc	-	-	136.3	Multi	341.9	h <sub>ref</sub>	Multimodal
1Mbe2006-2-F-A-578	156.4	154.7	Bi	123.4	0.237	nc	-	-	137.8	Bi	107.5	(h <sub>cv</sub> )	Multimodal
1Mbe2006-2-F-A-738	189.4	187.1	Multi	205	0.121	nc	-	-	103.6	Multi	106	h <sub>cv</sub>	Multimodal
1Mbe2006-2-F-A-778.2	53.23	52.94	Bi	20.3	0.185	nc	-	-	72.57	Uni	27.23	(h <sub>ref</sub> )	Multimodal
1Mbe2006-2-M-A-898.1	49.77	49.17	Bi-Multi	15.83	14.64	15.3463	Multi	5.781	43.15	Bi-Multi	14.11	h <sub>cv</sub>	Multimodal
1Mbe2006-3-F-A-917	149.7	148.9	Multi	218.6	0.294	nc	-	-	101.7	Multi	162.4	h <sub>cv</sub>	Multimodal
1Mbe2006-3-F-A-958	116.3	115	Bi	82.19	30.01	31.0126	Multi	24.88	63.19	Multi	47.46	h <sub>cv</sub>	Multimodal
1Mbe2006-3-F-A-977	116.7	117	Bi	131.5	0.21	nc	-	-	62.23	Multi	81.57	h <sub>cv</sub>	Multimodal
1Mbe2006-3-F-J-940	159.5	162	Bi	165.3	0.209	nc	-	-	80.74	Multi	83.28	h <sub>cv</sub>	Multimodal
1Mbe2006-3-M-J-597	94.51	93.92	Bi	52.61	0.144	nc	-	-	95.34	Bi	53.58	(h <sub>ref</sub> )	Multimodal
1Mbe2007-3-F-A-118	71.43	71.18	Bi	38.33	0.272	nc	-	-	46.9	Bi-Multi	27.92	h <sub>cv</sub>	Multimodal
1Mbe2007-3-F-A-138	318.8	323.2	Bi	592.1	0.149	nc	-	-	91.18	Multi	140.2	h <sub>cv</sub>	Multimodal
1Mbe2007-3-F-A-158	157.2	162	Bi-Multi	173.5	27.22	nc	-	-	86.04	Multi	98.07	h <sub>cv</sub>	Multimodal
1Mbe2007-3-F-J-337	105.4	105.2	Uni-Bi	79.67	0.208	nc	-	-	60.75	Multi	55.95	h <sub>cv</sub>	Multimodal
1Mbe2009-2-M-A-598	66.81	65.77	Uni-Bi	30.76	1.479	nc	-	-	68.75	Uni-Bi	32.09	(h <sub>ref</sub> )	Bimodal
1Mbe2009-3-F-A-338	147.6	148	Bi	130.3	0.222	nc	-	-	121	Bi	103.6	(h <sub>cv</sub> )	Multimodal
1Mbe2009-3-F-A-478	257.6	255.9	Bi	468.6	0.384	nc	-	-	121.9	Multi	255.1	h <sub>cv</sub>	Multimodal
1Mbe2009-3-F-A-738	161.3	157.4	Bi	128.5	0.252	nc	-	-	114.6	Bi	88.34	(h <sub>cv</sub> )	Multimodal
1Mbe2009-3-F-J-558	123.9	124.8	Bi	89.37	0.264	nc	-	-	76.02	Bi-Multi	52.17	h <sub>cv</sub>	Multimodal
1Mbe2009-3-F-J-638	271	270.6	Bi	394.6	14.15	nc	-	-	117.6	Bi-Multi	163.8	h <sub>cv</sub>	Multimodal
1Mbe2009-3-F-J-978	293	289.6	Bi	479.3	14.18	nc	-	-	91.65	Multi	147.6	h <sub>cv</sub>	Multimodal
2Mbe2006-1-F-A-263-2	63.64	78.27	Uni	25.27	14.99	15.5747	Multi	2.99	111.8	Uni	43.32	h <sub>LSCV</sub>	Multimodal
2Mbe2006-2-F-A-272	47.32	46.37	Bi	11	18.08	17.7525	Multi	4.081	21.01	Multi	4.78	h <sub>LSCV</sub>	Multimodal
2Mbe2006-2-F-A-274	564.5	564	Bi	1406	0.185	nc	-	-	272.9	Bi	372.7	(h <sub>cv</sub> )	Multimodal
2Mbe2006-3-F-A-748	24.72	25.56	Bi	4.553	10.23	7.97671	Multi	1.659	14	Bi-Multi	2.63	h <sub>cv</sub>	Multimodal
2Mbe2006-3-F-A-748.2	292	288.7	Bi	299.5	11.83	nc	-	-	31.39	Multi	9.617	h <sub>cv</sub>	Multimodal
2Mbe2006-3-F-A-901	104.5	103.8	Bi	61.04	0.146	nc	-	-	73.82	Bi-Multi	39.05	h <sub>cv</sub>	Multimodal
2Mbe2006-3-F-A-901.2	15.38	15.4	Uni-Bi	1.595	0.147	nc	-	-	9.847	Bi-Multi	1.133	h <sub>cv</sub>	Multimodal
2Mbe2007-3-M-A-178	57.41	56.45	Uni	19.34	0.14	nc	-	-	82.87	Uni	26.22	(h <sub>ref</sub> )	Multimodal
2Mbe2008-2-F-A-438	56.21	55.69	Uni	24.9	0.18	nc	-	-	72.69	Uni	31.95	(h <sub>ref</sub> )	Multimodal
2Mbe2008-2-F-A-478	65.92	65.63	Uni	29.7	12.72	13.0595	Multi	6.98	83.07	Uni	32.81	h <sub>LSCV</sub>	Multimodal
2Mbe2008-2-F-A-518	135	133.9	Uni-Bi	87.02	20.29	20.9713	Multi	12.69	39.98	Multi	24.7	(h <sub>LSCV</sub> )	Multimodal
2Mbe2008-2-F-A-738	53.91	58.96	Bi	22.47	25.9	25.074	Multi	9.046	66.84	Bi	26.01	h <sub>LSCV</sub>	Multimodal
2Mbe2008-2-F-PJ-498	184.7	185.7	Bi	154.9	0.123	nc	-	-	48.17	Bi	40.21	(h <sub>cv</sub> )	Multimodal
2Mbe2008-2-M-A-838	52.98	51.96	Multi	19.76	0.238	nc	-	-	72.22	Bi	26.87	h <sub>ref</sub>	Multimodal
2Mbe2008-3-F-A-618	64.02	64.33	Bi	36.13	0.313	nc	-	-	44.15	Multi	28.44	h <sub>cv</sub>	Multimodal
2Mbe2008-3-F-A-778	42.81	45.95	Bi	18.08	0.17	nc	-	-	47.25	Bi	18.61	h <sub>ref</sub> -h <sub>cv</sub>	Multimodal
2Mbe2008-3-F-A-818	51.22	54.28	Bi-Multi	22.23	0.177	nc	-	-	29.2	Multi	11.76	h <sub>cv</sub>	Multimodal
2Mbe2008-3-F-A-858	70.13	72.42	Bi	39.36	10.47	10.3148	Multi	4.675	55.88	Bi	31.21	h <sub>LSCV</sub> - (h <sub>cv</sub> )	Multimodal
2Mbe2008-3-F-A-898	65.58	65.12	Multi	30.7	61.07	64.531	Multi	30.44	92.9	Uni	42.1	(h <sub>cv</sub> )	Bimodal
2Mbe2008-3-F-J-758	163.2	162.9	Bi	155.6	4.612	nc	-	-	100.7	Bi	105.5	h <sub>cv</sub>	Multimodal
2Mbe2008-3-F-J-918	110.3	109.7	Bi-Multi	89.78	91.65	93.2262	Multi	78.1	156.3	Uni	119.4	h <sub>LSCV</sub>	Multimodal
2Mbe2008-3-M-J-718	52.27	54.57	Bi	19.25	0.163	nc	-	-	30.33	Bi-Multi	10.16	h <sub>cv</sub>	Multimodal
1Mna2009-2-F-A-119	76.41	75.64	Uni- Multi	44.88	0.187	nc	-	-	90.93	Uni	52.39	h <sub>ref</sub>	Multimodal
1Mna2009-2-F-A-139	149.5	149.7	Bi	149.9	37.45	36.1507	Multi	28.33	98.16	Multi	99.4	h <sub>cv</sub>	Multimodal
1Mna2009-2-F-A-158	157	156.9	Bi-Multi	128.9	0.452	nc	-	-	100.5	Multi	80.1	h <sub>cv</sub>	Multimodal
1Mna2009-2-F-A-179	155.2	153.7	Uni- Multi	160.2	71.64	71.6408	Multi	80.28	118.2	Multi	126.8	h <sub>LSCV</sub>	Multimodal
1Mna2009-2-F-A-219	634.8	620.5	Multi	2289	0.18	nc	-	-	399.8	Multi	1493	h <sub>cv</sub>	Multimodal
1Mna2009-2-F-A-238	70.05	71.13	Multi	32.27	10.06	10.131	Multi	2.443	48.58	Multi	21.23	h <sub>cv</sub>	Multimodal

1Mna2009-2-F-A-398	251.8	246.3	Uni-Bi	320.9	0.158	nc	-	-	174.6	Uni-Multi	236.3	$h_{CV}$	Multimodal
1Mna2009-3-F-A-697	93.47	101.1	Multi	69.95	0.185	nc	-	-	93.08	Multi	62.42	$h_{CV}$	Multimodal
1Mna2009-3-F-A-858	63.88	67.17	Bi	34.57	0.168	nc	-	-	74.72	Bi	38.32	$(h_{ref})$	Multimodal
1Mna2009-3-F-J-418	135.6	138.3	Multi	124.4	0.153	nc	-	-	88.19	Multi	74.39	$h_{CV}$	Multimodal
1Mna2009-3-F-J-458	3E+05	57.01	Uni	25.14	0.214	nc	-	-	73.6	Uni	32.35	$h_{ref}$	Unimodal
1Mna2009-3-F-J-497	566.9	569.5	Bi	1345	0.14	nc	-	-	818.3	Bi	2294	$(h_{ref})$	Multimodal
1Mna2009-3-F-J-599	280.2	288.2	Bi	542.9	31.67	nc	-	-	197.2	Multi	410.2	$h_{CV}$	Multimodal
1Mna2009-3-F-J-658	137.6	139.1	Bi-Multi	127.6	0.254	nc	-	-	146.7	Bi-Multi	134.7	$h_{ref}$	Multimodal
1Mna2009-3-F-J-677	102.6	114.4	Uni-Bi	73.98	23.53	19.5314	Multi	8.749	108.4	Uni-Bi	70	$(h_{CV})$	Multimodal
1Mna2009-3-F-J-898	99.19	116	Multi	66.58	22.88	21.4482	Multi	7.602	150.1	Multi	97.99	$(h_{ref})$	Multimodal
1Mna2009-3-F-J-918	121	122.8	Multi	115.9	16.33	15.7548	Multi	7.945	75.42	Multi	68.64	$h_{CV}$	Multimodal
1Paur2006-1-F-A-179	180.8	170.1	Uni-Bi	122.2	0.14	nc	-	-	75.87	Multi	47.41	$h_{CV}$	Multimodal
1Paur2006-1-F-A-419	274.3	278.8	Uni	314.9	462.3	402.371	Uni	579.8	333.7	Uni	397.4	$(h_{ref})$	Multimodal
1Paur2006-1-F-A-438	151.1	149.7	Bi	150.7	69.72	67.9156	Multi	79.65	123.6	Bi	129.3	$h_{LSCV}$	Multimodal
1Paur2006-1-F-A-458	320.5	324.7	Uni-Bi	467.7	375.4	330.978	Uni-Bi	477.9	400.7	Uni	597.8	$(h_{ref})$	Multimodal
1Paur2006-1-M-A-118	109.6	106.9	Uni	73.61	77.19	71.1919	Multi	51.06	125.7	Uni	84.71	$h_{LSCV}$	Multimodal
1Paur2006-1-M-A-138	55.56	53.77	Uni-Bi	15.72	0.179	nc	-	-	46.97	Multi	13.79	$h_{CV}$	Multimodal
1Paur2006-1-M-A-278	185.9	183.4	Uni	175.3	31.93	31.927	Multi	21.12	122	Bi-Multi	115.8	$h_{CV}$	Multimodal
1Paur2006-2-F-A-498	282.5	286.7	Bi	362.5	25.82	nc	-	-	182.6	Bi-Multi	216.4	$h_{CV}$	Multimodal
1Paur2006-2-F-A-798	380.5	325.9	Bi	544.8	275.9	nc	-	-	475.6	Uni	544.8	$(h_{ref})$	Multimodal
1Paur2006-2-F-A-838	126.9	123.7	Uni-	93.98	8.185	nc	-	-	81.22	Multi	54.35	$h_{CV}$	Multimodal
1Paur2006-2-M-A-198	137.8	138.9	Uni-Bi	82.79	0.148	nc	-	-	70.64	Bi	38.88	$(h_{CV})$	Multimodal
1Paur2006-2-M-A-898.2	117.6	114.8	Bi	65.86	50.23	50.4227	Multi	25.4	63.13	Bi-Multi	32.37	$h_{CV}$	Bimodal
1Paur2006-3-F-A-858	75.54	74.75	Bi	28.61	23.64	20.161	Multi	6.371	44.61	Bi-Multi	15.64	$h_{CV}$	Multimodal
1Paur2006-3-M-A-877	36.13	35.78	Uni	8.494	15.66	15.2148	Multi	4.518	18.89	Multi	5.327	$h_{LSCV}$	Multimodal
1Paur2006-3-M-J-537	341.3	338.7	Uni	686.1	59.09	43.45	Multi	72.22	211.5	Bi-Multi	454.9	$h_{CV}$	Multimodal
1Paur2007-1-F-A-058	203.4	208.9	Bi	236.5	0.136	nc	-	-	113.9	Multi	127.4	$h_{CV}$	Multimodal
1Paur2007-1-F-A-078	187.7	190.6	Uni	248.9	28.11	29.8382	Multi	51.08	137.1	Uni-Bi	199.2	$(h_{CV})$	Multimodal
1Paur2007-2-F-A-118	108	107.1	Uni-Bi	90.66	2.001	nc	-	-	86.6	Multi	75.45	$h_{CV}$	Multimodal
1Paur2007-2-M-A-100	138.6	134.6	Uni	108.5	25.71	nc	-	-	84.11	Multi	69.09	$(h_{ref})$	Bimodal
1Paur2009-1-F-A-055	73.46	73.47	Uni	40.62	0.204	nc	-	-	73.46	Uni	40.62	$(h_{ref}-h_{CV})$	Multimodal
1Paur2009-1-F-A-096	89.02	90.85	Multi	47.1	0.146	nc	-	-	71.69	Multi	35.22	$h_{CV}$	Multimodal
1Paur2009-1-F-A-355	53.01	52.97	Uni-Bi	17.81	16.63	15.0341	Multi	4.871	17.66	Multi	5.773	$h_{LSCV}$	Multimodal
1Paur2009-1-F-A-696	63.17	62.68	Uni	26.19	0.188	nc	-	-	35.36	Multi	15.65	$h_{CV}$	Bimodal
1Paur2009-1-F-A-897	50.81	50.01	Bi	13.29	0.189	nc	-	-	20.36	Multi	5.218	$h_{CV}$	Multimodal
1Paur2009-1-F-A-977	108.4	108.1	Bi-Multi	62.78	0.158	nc	-	-	74.09	Multi	40.31	$h_{CV}$	Multimodal
1Paur2009-1-M-A-037	54.22	55.27	Bi	19.5	8.667	7.87188	Multi	2.83	23.53	Multi	9.997	$h_{CV}$	Multimodal
1Paur2009-1-M-A-857	159.7	40.82	Bi-Multi	9.445	9.049	nc	-	-	215.1	Bi-Multi	9.488	$h_{ref}-h_{CV}$	Bimodal
1Paur2009-2-F-A-038	121.4	119.9	Multi	80.09	0.166	nc	-	-	124.6	Multi	84.4	$h_{ref}$	Multimodal
1Paur2009-2-F-A-058	158.5	157.2	Uni	123.5	0.133	nc	-	-	228.8	Uni	221.2	$(h_{ref})$	Multimodal
1Paur2009-2-F-A-077	170.8	162.6	Uni	115	144.5	nc	-	-	162.9	Uni	115.2	$(h_{ref}-h_{CV})$	Multimodal
1Paur2009-2-F-A-197	154.8	151.9	Bi	105.7	0.17	nc	-	-	79.95	Bi-Multi	47.14	$h_{CV}$	Multimodal
1Paur2009-2-F-A-716	204.4	203	Bi	229.5	0.161	nc	-	-	69.38	Multi	75.55	$h_{CV}$	Multimodal
1Paur2009-2-M-A-017	458.1	429.3	Uni	850.2	27.64	nc	-	-	532.9	Uni	1079	$(h_{ref})$	Multimodal
1Paur2009-2-M-A-578	159.7	163	Uni-Bi	156.7	9.049	nc	-	-	215.1	Uni	208.1	$(h_{ref})$	Multimodal
1Paur2009-3-F-A-838	187.2	186.4	Bi	210.3	0.152	nc	-	-	91.7	Multi	85.8	$h_{CV}$	Multimodal
1Paur2009-3-F-J-398	124.5	133.9	Bi	209.4	0.138	nc	-	-	52.25	Multi	24.7	$h_{ref}$	Bimodal
1Paur2009-3-F-PJ-618	128.3	128.5	Uni-Bi	104.4	22.65	21.9435	Multi	17.69	124.8	Uni-Bi	101.4	$(h_{CV})$	Multimodal
1Paur2009-3-M-J-798	50.56	50.94	Uni-Bi	14.17	0.306	nc	-	-	42.08	Uni-Bi	11.52	$h_{CV}$	Bimodal
2Paur2006-1-F-A-262	67.44	69.7	Bi	22.51	0.172	nc	-	-	94.42	Bi	34.66	$(h_{ref})$	Multimodal
2Paur2006-1-F-A-266	46.55	46.44	Bi	16.82	0.14	nc	-	-	34.01	Multi	12.49	$h_{CV}$	Multimodal
2Paur2007-1-F-A-199	113.5	113.4	Uni-Bi	80.22	100.9	91.4882	Uni-Bi	68.54	106.4	Uni-Bi	76.36	$h_{LSCV}$	Bimodal
2Paur2007-1-F-A-299	156	155.9	Bi	143.1	0.281	nc	-	-	76.99	Multi	77.44	$h_{CV}$	Multimodal
2Paur2007-1-F-A-379	126	125.5	Uni-Bi	115.8	71.65	19.6506	Bi-Multi	17.24	152.1	Uni	133	$(h_{ref}-h_{CV})$	Bimodal
2Paur2007-1-F-A-399	95.28	96.77	Bi	63.92	78.37	12.4144	Bi-Multi	6.981	106.7	Bi	69.7	$h_{LSCV}$	Multimodal
2Paur2007-1-M-A-179	218.3	216	Multi	353.4	60.54	52.1454	Multi	72.55	244.6	Multi	161.7	$(h_{ref}-h_{CV})$	Multimodal
2Paur2007-3-F-A-058	161.5	156.7	Uni	141.7	65.51	46.7071	Multi	39.42	162.7	Uni	146.8	$(h_{ref})$	Bimodal
2Paur2007-3-F-A-098	106.4	105.1	Uni	82.94	0.152	nc	-	-	111.7	Uni	86.58	$(h_{ref})$	Multimodal
2Paur2007-3-F-A-278	152.6	151	Bi-Multi	137.9	0.138	nc	-	-	97.69	Bi-Multi	87.89	$h_{CV}$	Multimodal

2Paur2007-3-F-A-378	79.6	79.17	Bi	38.91	0.138	nc	-	-	44.56	<u>Multi</u>	24.53	$h_{CV}$	Multimodal
2Paur2007-3-F-A-438	62.11	62.01	Uni-Bi	24.87	0.286	nc	-	-	38.73	Multi	18.28	$h_{ref}$	Unimodal
2Paur2008-2-F-A-458	85.71	84.96	Bi	53.36	0.161	nc	-	-	69.01	Multi	25.24	$h_{CV}$	Multimodal
2Paur2008-2-F-A-558	126.5	125.1	Bi	73.6	0.14	nc	-	-	55.99	<u>Bi-Multi</u>	23.48	$h_{CV}$	Multimodal
2Paur2008-2-F-A-638	70.23	67.97	<u>Bi</u>	24.33	33.03	26.9817	Multi	9.12	95.74	Uni-Bi	35.9	$h_{ref}$	Bimodal
2Paur2008-2-F-A-738	52.69	53.92	Uni	16.97	25.6	22.1672	<u>Multi</u>	6.83	50.53	Uni	15.96	$h_{LSCV}$	Multimodal
2Paur2008-2-F-A-838	42.57	44.17	Uni	8.601	0.138	nc	-	-	44.38	Uni	8.649	$(h_{ref}-h_{CV})$	Multimodal
2Paur2008-2-F-A-938	64.19	64.32	<u>Multi</u>	32.22	9.045	7.34144	Multi	1.977	76.8	Multi	38.1	$h_{ref}$	Multimodal
2Paur2008-2-M-PJ-638	859.5	850.5	Bi	2971	176.6	157.214	<u>Multi</u>	294.2	309.4	Multi	731.3	$h_{LSCV}$	Multimodal
2Paur2008-3-F-A-537	377.3	374.8	Bi	611.4	21.12	nc	-	-	67.2	Multi	80.56	$h_{CV}$	Multimodal
2Paur2008-3-F-A-577	35.27	40.58	Multi	15.69	0.174	nc	-	-	39.31	Multi	15.33	$h_{CV}-h_{ref}$	Multimodal
2Paur2008-3-F-A-657	373.7	361.4	Multi	640	4.085	nc	-	-	329.3	<u>Multi</u>	560.5	$h_{CV}$	Multimodal
2Paur2008-3-F-A-797	730.9	727.3	Bi-Multi	2398	51.7	nc	-	-	100.3	Multi	118.6	$h_{CV}$	Multimodal
2Paur2008-3-F-A-977	761.2	755.8	Bi	2256	0.164	nc	-	-	227.3	<u>Multi</u>	307.4	$h_{CV}$	Multimodal
2Paur2008-3-M-A-697	184	181.4	Bi	141.5	35.88	33.5367	Multi	22.35	106.1	<u>Bi-Multi</u>	73.84	$h_{CV}$	Multimodal
1Ppi2007-1-M-A-019	91.39	118.3	Bi	54.4	0.155	nc	-	-	135.9	Bi	66.64	$h_{ref}$	Multimodal
1Ppi2007-1-M-A-219	398.4	395.7	<u>Multi</u>	1037	0.168	nc	-	-	452.8	Multi	1212	$h_{ref}$	Multimodal
1Ppi2007-2-F-A-278	693.1	704.6	Bi	4166	19.63	nc	-	-	145.3	<u>Multi</u>	160.9	$h_{CV}$	Multimodal
1Ppi2007-2-M-A-100	115	113.4	Bi	67.33	10.31	nc	-	-	127.7	Bi	78.17	$(h_{ref})$	Multimodal
1Ppi2007-2-M-A-258	210.8	181.5	Uni	126.2	381.1	nc	-	-	289.5	Uni	179.8	$(h_{ref})$	Multimodal
1Ppi2007-3-F-A-419	143.1	147.4	Uni-Bi	129	0.169	nc	-	-	76.3	<u>Multi</u>	77.15	$h_{CV}$	Multimodal
1Ppi2007-3-M-A-319	77.17	75.37	<u>Multi</u>	38.07	0.153	nc	-	-	88.99	Multi	45.05	$h_{ref}$	Multimodal
1Ppi2007-3-M-A-359	199.5	195.6	<u>Bi-Multi</u>	242.5	0.158	nc	-	-	244	Bi-Multi	308	$h_{ref}$	Multimodal

**Annexe 4 (Chapitre 6) : Taille des DV calculés par les Kernels 50 et 95%.** Ces calculs sont présentés pour chaque individu, en ha, à partir des résultats des tests opérés sur le type de représentation, et sur les calculs du meilleur facteur de lissage répondant le mieux au modèle de représentation du DV. Pour chaque animal est aussi présenté le sexe (M pour mâle et F pour Femelle), l'âge (A pour Adulte, J pour juvénile ou jeune de l'année), des éléments sur l'état de l'animal (longueur de l'avant-bras AB, poids au moment de la capture, et l'état sexuel : VNA vierge non actif, ANA adulte non actif, GES ou (GES) pour gestante ou gestante supposée, ALL pour allaitante, AVO pour les femelles ayant avorté, PAL pour post-allaitante, AAC pour les adultes actifs sexuellement, ? quand nous n'avons pas pu le déterminer).

ID	Sexe	Age	AB (en mm)	Poids (en gr.)	Etat sexuel	Nb locs R	Modèle valide/retenu	Valeur de h	Forme du modèle	K50	K95
<b><i>Myotis bechsteinii</i></b>											
1Mbe2006-1-M-A-478	M	A	42.5	7.9	ANA	105	h <sub>CV</sub>	42.968	Multi	2.932366	30.83714
1Mbe2006-2-F-A-558	F	A	43.8	11	ALL	20	h <sub>ref</sub>	86.009	Multi	3.828659	60.54623
1Mbe2006-2-F-A-578	F	A	41.2	9.7	ALL	42	(h <sub>CV</sub> )	137.82	Bi	25.81123	107.4686
1Mbe2006-2-F-A-738	F	A	42.5	11	ALL	49	h <sub>CV</sub>	103.64	Multi	19.87306	105.9896
1Mbe2006-2-F-A-778.2	F	A	39.5	9.2	ALL	56	(h <sub>ref</sub> )	52.945	Bi	4.021982	20.29554
1Mbe2006-2-M-A-898.1	M	A	38.5	8.5	ANA	35	h <sub>CV</sub>	43.152	Bi-Multi	3.381085	14.10506
1Mbe2006-3-F-A-917	F	A	40.1	10	fin AAC	116	h <sub>CV</sub>	101.73	Multi	17.10854	162.3566
1Mbe2006-3-F-A-958	F	A	43	10	VNA	55	h <sub>CV</sub>	63.195	Multi	10.57054	47.45957
1Mbe2006-3-F-A-977	F	A	42	9.8	VNA	149	h <sub>CV</sub>	62.225	Multi	5.791896	81.56921
1Mbe2006-3-F-J-940	F	J	41.5	9.9	VNA	120	h <sub>CV</sub>	80.742	Multi	7.335146	83.27548
1Mbe2006-3-M-J-597	M	J	41	9	VNA	57	(h <sub>ref</sub> )	93.917	Bi	8.134629	52.60983
1Mbe2007-3-F-A-118	F	A	47	9.3	ALL	56	h <sub>CV</sub>	46.901	Bi-Multi	6.404924	27.92295
1Mbe2007-3-F-A-138	F	A	43	9.8	ALL	44	h <sub>CV</sub>	91.182	Multi	23.89617	140.2143
1Mbe2007-3-F-A-158	F	A	46	9.1	ALL	47	h <sub>CV</sub>	86.039	Multi	21.24979	98.0672
1Mbe2007-3-F-J-337	F	J	39.9	7.8	VNA	54	h <sub>CV</sub>	60.746	Multi	15.2436	55.95459
1Mbe2009-2-M-A-598	M	A	41,8	9,9	ANA	39	(h <sub>ref</sub> )	65.767	Uni-Bi	5.382065	30.76306
1Mbe2009-3-F-A-338	F	A	42,6	9,9	ANA	70	(h <sub>CV</sub> )	121	Bi	10.5495	103.5574
1Mbe2009-3-F-A-478	F	A	41,7	9,2	ANA	69	h <sub>CV</sub>	121.89	Multi	49.96046	255.1379
1Mbe2009-3-F-A-738	F	A	44,5	11	ALL	46	(h <sub>CV</sub> )	114.57	Bi	13.38989	88.34415
1Mbe2009-3-F-J-558	F	J	42,9	9,2	VNA	60	h <sub>CV</sub>	76.015	Bi-Multi	5.313714	52.17101
1Mbe2009-3-F-J-638	F	J	42,1	9,7	VNA	31	h <sub>CV</sub>	117.58	Bi-Multi	31.84251	163.8274
1Mbe2009-3-F-J-978	F	J	42,3	9,1	VNA	51	h <sub>CV</sub>	91.645	Multi	16.69541	147.6226
2Mbe2006-1-F-A-263-2	F	A	40,3	9,25	?	38	h <sub>LSCV</sub>	15.575	Multi	0.45125	2.989531
2Mbe2006-2-F-A-272	F	A	43.5	11	PAL	33	h <sub>LSCV</sub>	17.752	Multi	0.928017	4.080733
2Mbe2006-2-F-A-274	F	A	44	10	PAL	39	(h <sub>CV</sub> )	272.9	Bi	73.76589	372.6893
2Mbe2006-3-F-A-748	F	A	41.25	9.5	PAL	62	h <sub>CV</sub>	13.996	Bi-Multi	0.714339	2.630232
2Mbe2006-3-F-A-748.2	F	A	43.6	10.5	ANA	51	h <sub>CV</sub>	31.389	Multi	0.843578	9.616787
2Mbe2006-3-F-A-901	F	A	?	?	ANA	59	h <sub>CV</sub>	73.816	Bi-Multi	6.614367	39.04798
2Mbe2006-3-F-A-901.2	F	A	44.25	11.5	PAL	54	h <sub>CV</sub>	9.8472	Bi-Multi	0.229165	1.133136
2Mbe2007-3-M-A-178	M	A	41.1	9.3	ANA	40	(h <sub>ref</sub> )	56.452	Uni	3.300039	19.33894
2Mbe2008-2-F-A-438	F	A	43.3	11.5	GES	73	(h <sub>ref</sub> )	55.695	Uni	3.744594	24.90155
2Mbe2008-2-F-A-478	F	A	40.4	8.5	ANA	58	h <sub>LSCV</sub>	13.06	Multi	1.628679	6.980051
2Mbe2008-2-F-A-518	F	A	40.5	9.3	ANA	48	h <sub>CV</sub> -(h <sub>LSCV</sub> )	39.977	Multi	4.821955	24.70325
2Mbe2008-2-F-A-738	F	A	41.15	10.5	(GES)	43	h <sub>LSCV</sub>	25.074	Multi	1.439787	9.045617
2Mbe2008-2-F-PJ-498	F	PJ	43.05	10.1	VNA	32	(h <sub>CV</sub> )	48.171	Bi	9.160727	40.21404
2Mbe2008-2-M-A-838	M	A	41.6	9	ANA	32	h <sub>ref</sub>	51.964	Multi	3.140325	19.76267
2Mbe2008-3-F-A-618	F	A	43	8.9	ANA	90	h <sub>CV</sub>	44.153	Multi	3.287127	28.43625
2Mbe2008-3-F-A-778	F	A	40.6	9.1	ANA	76	h <sub>ref</sub> -h <sub>CV</sub>	45.955	Bi	2.531691	18.07841
2Mbe2008-3-F-A-818	F	A	42	10	ALL	56	h <sub>CV</sub>	29.199	Multi	2.068295	11.76343
2Mbe2008-3-F-A-858	F	A	42.5	9.5	PAL	73	h <sub>LSCV</sub> -(h <sub>CV</sub> )	10.315	Multi	0.821358	4.67542
2Mbe2008-3-F-A-898	F	A	44.3	9.85	ANA	35	(h <sub>CV</sub> )	92.904	Uni	8.210715	42.09755
2Mbe2008-3-F-J-758	F	J	41.6	8.7	VNA	79	h <sub>CV</sub>	100.72	Bi	14.10121	105.4979
2Mbe2008-3-F-J-918	F	J	42.2	9.9	VNA	31	h <sub>LSCV</sub>	93.226	Multi	14.28943	78.09757
2Mbe2008-3-M-J-718	M	J	39.6	7.7	VNA	60	h <sub>CV</sub>	30.332	Bi-Multi	1.2596	10.1594

**Myotis nattereri**

1Mna2009-2-F-A-119	F	A	41,1	9,4	ALL	63	$h_{ref}$	75.636	Uni-Multi	4.911962	44.87747
1Mna2009-2-F-A-139	F	A	40,2	8,5	ALL	43	$h_{CV}$	98.156	Multi	11.80502	99.39823
1Mna2009-2-F-A-158	F	A	38,4	8	ALL	29	$h_{CV}$	100.49	Multi	12.48292	80.09875
1Mna2009-2-F-A-179	F	A	40,1	9,2	ALL	38	$h_{LSCV}$	71.641	Multi	15.2305	80.27743
1Mna2009-2-F-A-219	F	A	39,8	8,4	ALL	29	$h_{CV}$	399.8	Multi	226.9587	1492.963
1Mna2009-2-F-A-238	F	A	39,6	8,7	(ALL)	76	$h_{CV}$	48.583	Multi	1.769217	21.2306
1Mna2009-2-F-A-398	F	A	37,5	7,4	ALL	23	$h_{CV}$	174.63	Uni-Multi	52.91897	236.2933
1Mna2009-3-F-A-697	F	A	40,8	8,8	ALL	40	$h_{CV}$	93.077	Multi	6.043534	62.41683
1Mna2009-3-F-A-858	F	A	40,3	8,7	ANA	59	( $h_{ref}$ )	67.174	Bi	4.613837	34.56657
1Mna2009-3-F-J-418	F	J	39,8	7,3	VNA	44	$h_{CV}$	88.188	Multi	7.860586	74.38799
1Mna2009-3-F-J-458	F	J	39,4	7,4	VNA	56	$h_{ref}$	57.01	Uni	2.946794	25.13796
1Mna2009-3-F-J-497	F	J	40,8	7,9	VNA	12	( $h_{ref}$ )	569.46	Bi	250.7131	1345.206
1Mna2009-3-F-J-599	F	J	37,1	6,8	VNA	48	$h_{CV}$	197.21	Multi	57.12297	410.2059
1Mna2009-3-F-J-658	F	J	39,7	7,5	VNA	31	$h_{ref}$	139.13	Bi-Multi	23.32252	127.6236
1Mna2009-3-F-J-677	F	J	42	7,7	VNA	25	( $h_{CV}$ )	108.39	Uni-Bi	11.26922	69.99514
1Mna2009-3-F-J-898	F	J	40,9	7,95	VNA	23	( $h_{ref}$ )	116.03	Multi	9.439506	66.57775
1Mna2009-3-F-J-918	F	J	38,2	7,1	VNA	66	$h_{CV}$	75.418	Multi	6.121694	68.64112

**Plecotus auritus**

1Paur2006-1-F-A-179	F	A	37.5	8.2	?	12	$h_{CV}$	75.873	Multi	11.52034	47.40669
1Paur2006-1-F-A-419	M	A	?	?	?	8	( $h_{ref}$ )	278.76	Uni	88.99321	314.94
1Paur2006-1-F-A-438	F	A	40.9	7.8	?	61	$h_{LSCV}$	67.916	Multi	17.03243	79.6469
1Paur2006-1-F-A-458	F	A	39.6		?	11	( $h_{ref}$ )	324.75	Uni-Bi	111.3414	467.6986
1Paur2006-1-M-A-118	M	A	36.45	6.4	ANA	24	$h_{LSCV}$	71.192	Multi	9.623236	51.05831
1Paur2006-1-M-A-138	M	A	38.2	6.55	ANA	19	$h_{CV}$	46.971	Uni-Multi	5.376714	13.79218
1Paur2006-1-M-A-278	M	A	?	?	?	33	$h_{CV}$	122.04	Bi-Multi	13.67986	115.8139
1Paur2006-2-F-A-498	F	A	39.9	7.5	GES	16	$h_{CV}$	182.59	Bi-Multi	39.51953	216.4312
1Paur2006-2-F-A-798	F	A	39.1	9	GES	5	( $h_{ref}$ )	325.94	Bi	73.81981	544.8315
1Paur2006-2-F-A-838	F	A	35.85	7.5	ALL	22	$h_{CV}$	81.218	Multi	7.357816	54.34891
1Paur2006-2-M-A-198	M	A	38.05	6.6	ANA	20	( $h_{CV}$ )	70.637	Bi	9.376923	38.88472
1Paur2006-2-M-A-898.2	M	A	36.1	6.8	ANA	22	$h_{CV}$	63.134	Bi-Multi	6.12324	32.3733
1Paur2006-3-F-A-858	F	A	39	7.3	VNA	18	$h_{CV}$	44.605	Bi-Multi	3.940002	15.6424
1Paur2006-3-M-A-877	M	A	37.7	6.85	ANA	47	$h_{LSCV}$	15.215	Multi	1.153403	4.518024
1Paur2006-3-M-J-537	M	J	38.8	9.5	VNA	32	$h_{CV}$	211.48	Bi-Multi	102.1043	454.9036
1Paur2007-1-F-A-058	F	A	38	6.5	(GES)	25	$h_{CV}$	113.87	Multi	24.63171	127.3719
1Paur2007-1-F-A-078	F	A	38.25	6.95	(GES)	65	( $h_{CV}$ )	137.14	Uni-Bi	43.31689	199.2168
1Paur2007-2-F-A-118	F	A	39.1	7.8	GES	52	$h_{CV}$	86.597	Multi	8.286951	75.44836
1Paur2007-2-M-A-100	M	A	37.2	6.5	ANA	24	( $h_{ref}$ )	134.59	Uni	20.25124	108.4699
1Paur2009-1-F-A-055	F	A	38,3	8,1	ANA	68	( $h_{ref}$ - $h_{CV}$ )	73.471	Uni	7.192716	40.61769
1Paur2009-1-F-A-096	F	A	38,3	8,2	ANA	27	$h_{CV}$	71.693	Multi	6.852022	35.21692
1Paur2009-1-F-A-355	F	A	40,8	8,3	ANA	46	$h_{LSCV}$	15.034	Multi	1.209148	4.870652
1Paur2009-1-F-A-696	F	A	37,45	7,5	ANA	40	$h_{CV}$	35.361	Multi	2.685267	15.64962
1Paur2009-1-F-A-897	F	A	40	8,3	?	43	$h_{CV}$	20.364	Multi	0.891662	5.217871
1Paur2009-1-F-A-977	F	A	37,5	7,6	?	27	$h_{CV}$	74.088	Multi	8.560528	40.30582
1Paur2009-1-M-A-037	M	A	39,4	9,3	ANA	49	$h_{CV}$	23.526	Multi	2.287907	9.997394
1Paur2009-1-M-A-857	M	A	38,8	7,3	ANA	20	( $h_{ref}$ - $h_{CV}$ )	215.05	Bi-Multi	1.893748	9.487822
1Paur2009-2-F-A-038	F	A	39,2	8,7	ALL	48	$h_{ref}$	119.89	Multi	9.76068	80.09499
1Paur2009-2-F-A-058	F	A	41,8	9,8	AAC	35	( $h_{ref}$ )	157.18	Uni	22.98048	123.5431
1Paur2009-2-F-A-077	F	A	38,9	7,6	GES	11	( $h_{ref}$ - $h_{CV}$ )	162.6	Uni	29.4915	114.9916
1Paur2009-2-F-A-197	F	A	37,8	11	ALL	34	$h_{CV}$	79.951	Bi-Multi	6.734349	47.14044
1Paur2009-2-F-A-716	F	A	39,5	7,9	ALL	92	$h_{CV}$	69.384	Multi	8.982414	75.54852
1Paur2009-2-M-A-017	M	A	37,2	8	AAC	10	( $h_{ref}$ )	429.32	Uni	227.3556	850.1858
1Paur2009-2-M-A-578	M	A	39,1	12	ANA	49	( $h_{ref}$ )	163.04	Uni-Bi	29.16309	156.6972
1Paur2009-3-F-A-838	F	A	37,2	9	PAL	30	$h_{CV}$	91.698	Multi	10.63976	85.79901
1Paur2009-3-F-J-398	F	J	38,7	7,2	VNA	22	$h_{ref}$	133.94	Bi	18.1598	209.4103
1Paur2009-3-F-PJ-618	F	PJ	40,8	9,2	PAL	47	( $h_{CV}$ )	124.76	Uni-Bi	21.08807	101.3588
1Paur2009-3-M-J-798	M	J	37,7	7,5	VNA	47	$h_{CV}$	42.082	Uni-Bi	2.803503	11.51985
2Paur2006-1-F-A-262	F	A	?	?	ANA	18	( $h_{ref}$ )	69.699	Bi	4.520531	22.50544
2Paur2006-1-F-A-266	F	A	?	?	ANA	69	$h_{CV}$	34.006	Multi	1.33779	12.48604
2Paur2007-1-F-A-199	F	A	41	8.3	(GES)	32	$h_{LSCV}$	91.488	Uni-Bi	18.3075	68.53576

2Paur2007-1-F-A-299	F	A	40.7	8.2	ANA	74	$h_{CV}$	76.994	<u>Multi</u>	17.71402	77.44482
2Paur2007-1-F-A-379	F	A	39	7.9	(GES)	38	$(h_{ref}-h_{LSCV})$	152.07	Uni	29.71198	132.9857
2Paur2007-1-F-A-399	F	A	40.05	8.3	(GES)	38	$h_{LSCV}$	106.72	Bi	14.28917	69.70062
2Paur2007-1-M-A-179	M	A	37.15	6.9	VNA	44	$(h_{ref}-h_{CV})$	244.56	Multi	25.29238	161.7381
2Paur2007-3-F-A-058	F	A	38.1	6.9	ANA	22	$(h_{ref})$	156.75	Uni	30.16333	141.7198
2Paur2007-3-F-A-098	F	A	38.5	7.15	ANA	41	$(h_{ref})$	105.1	Uni	16.33167	82.93732
2Paur2007-3-F-A-278	F	A	39.4	7.8	PAL	33	$h_{CV}$	97.687	Bi- <u>Multi</u>	15.91548	87.88795
2Paur2007-3-F-A-378	F	A	37.9	7.2	PAL	37	$h_{CV}$	44.561	<u>Multi</u>	4.928827	24.52884
2Paur2007-3-F-A-438	F	A	38	7.1	PAL	41	$h_{ref}$	62.013	Uni-Bi	7.391247	24.866
2Paur2008-2-F-A-458	F	A	41	12	ALL	53	$h_{CV}$	69.006	Multi	3.278921	25.23776
2Paur2008-2-F-A-558	F	A	39.6	8.9	ANA	53	$h_{CV}$	55.99	Bi- <u>Multi</u>	3.572809	23.47846
2Paur2008-2-F-A-638	F	A	39.1	11.5	GES	17	$h_{ref}$	67.969	Bi	5.483635	24.33363
2Paur2008-2-F-A-738	F	A	38.55	7.9	GES	23	$h_{LSCV}$	22.167	<u>Multi</u>	1.663456	6.829767
2Paur2008-2-F-A-838	F	A	40	7.8	ANA	10	$(h_{ref}-h_{CV})$	44.384	Uni	2.3356	8.64907
2Paur2008-2-F-A-938	F	A	38.65	7.3	AVO	62	$h_{ref}$	64.319	Uni- <u>Multi</u>	5.34328	32.21998
2Paur2008-2-M-PJ-638	M	PJ	38.8	6.25	VNA	23	$h_{LSCV}$	157.21	<u>Multi</u>	56.25179	294.2401
2Paur2008-3-F-A-537	F	A	37.7	8.1	PAL	62	$h_{CV}$	67.196	Multi	17.10017	80.5608
2Paur2008-3-F-A-577	F	A	39.5	8.1	PAL	91	$h_{CV}-h_{ref}$	39.309	Multi	2.304618	15.33228
2Paur2008-3-F-A-657	F	A	37.7	8.15	PAL	20	$h_{CV}$	329.31	<u>Multi</u>	75.63382	560.466
2Paur2008-3-F-A-797	F	A	38.4	8.1	PAL	47	$h_{CV}$	100.29	Multi	21.56274	118.5951
2Paur2008-3-F-A-977	F	A	40	7.8	PAL	75	$h_{CV}$	227.3	<u>Multi</u>	46.10861	307.3907
2Paur2008-3-M-A-697	M	A	38.2	7.7	ANA	40	$h_{CV}$	106.06	Bi- <u>Multi</u>	12.44848	73.84213
<b><i>Pipistrellus pipistrellus</i></b>											
1Ppi2007-1-M-A-019	M	A	30.5	4.15	AAC	43	$h_{ref}$	118.33	Bi	8.588905	54.3964
1Ppi2007-1-M-A-219	M	A	30.1	4.65	ANA	42	$h_{ref}$	395.71	<u>Multi</u>	136.4595	1036.567
1Ppi2007-2-F-A-278	F	A	32	6	ALL	21	$h_{CV}$	145.32	<u>Multi</u>	29.75585	160.8676
1Ppi2007-2-M-A-100	M	A	33	4.8	ANA	21	$(h_{ref})$	113.4	Bi	13.39784	67.32653
1Ppi2007-2-M-A-258	M	A	31.4	4.8	ANA	5	$(h_{ref})$	181.52	Uni	30.33578	126.1533
1Ppi2007-3-F-A-419	F	A	33.3	5.5	ALL	30	$h_{CV}$	76.302	<u>Multi</u>	15.49511	77.14588
1Ppi2007-3-M-A-319	M	A	31.3	5.5	AAC	29	$h_{ref}$	75.369	<u>Multi</u>	4.76347	38.06806
1Ppi2007-3-M-A-359	M	A	31.7	4.95	AAC	27	$h_{ref}$	195.61	Bi- <u>Multi</u>	40.95865	242.5076

## Annexe 5 (Chapitre 2) : Valeur des PSI par paire d'individus dans les différents groupes étudiés.

- *M. nattereri* (Pecqueuse, FD de Rambouillet, juillet 2009).

	179/158	179/119	179/398	179/139	179/219	179/238	158/119	158/398	158/139	158/219	158/238	119/398	119/139	119/219	119/238	398/139	398/219	398/238	139/219	139/238	219/238
OSP	0.67	0.33	0.5	1	0.33	0.67	1	0.5	0.5	0.5	0.5	0	0.5	0.33	0.33	0	0	0	1	0.5	0.67
Bat1 roosts/day	0.75	0.75	0.75	0.75	0.75	0.75	0.67	0.67	0.67	0.67	0.67	0.33	0.33	0.33	0.33	0.5	0.5	0.5	1	1	0.5
Bat2 roosts/day	0.67	0.33	0.5	1	0.5	1	0.33	0.5	1	0.5	1	0.5	1	0.5	1	1	0.5	1	0.5	1	1
ESP	0.22	0.45	0.67	0.33	0.3	0.15	1.13	0.75	1.49	0.75	0.37	6.06	0.76	0.67	0.34	2	4	2	0.5	0.25	0.22
<b>PSI</b>	<b>0.45</b>	<b>-0.1</b>	<b>-0.2</b>	<b>0.67</b>	<b>0.04</b>	<b>0.52</b>	<b>-0.1</b>	<b>-0.2</b>	<b>-1</b>	<b>-0.2</b>	<b>0.13</b>	<b>-6.1</b>	<b>-0.3</b>	<b>-0.3</b>	<b>-0</b>	<b>-2</b>	<b>-4</b>	<b>-2</b>	<b>0.5</b>	<b>0.25</b>	<b>0.44</b>

- *M. nattereri* (Pecqueuse, FD de Rambouillet, août 2009).

	418/458	418/497	418/599	418/658	418/677	418/697	418/858	418/898	418/918	458/497	458/599	458/658	458/677	458/697	458/858	458/898	458/918	497/599	497/658	497/677	497/697	497/858	497/898	497/918
OSP	0.33	0.2	0.2	0.25	0.25	0.5	0.67	0.25	0.4	0.33	0.67	1	0.33	0.67	0.5	0.33	0.33	0.4	0.25	0.25	0.25	0.33	0.25	0.2
Bat1 roosts/day	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0.6	0.6	0.6	0.6	0.6	0.6	0.6
Bat2 roosts/day	1	0.6	1	1	1	1	1	1	0.6	1	1	1	1	1	1	1	0.6	1	1	1	1	1	1	0.6
ESP	0.11	0.067	0.04	0.06	0.06	0.06	0.11	0.06	0.07	0.11	0.11	0.11	0.11	0.11	0.25	0.11	0.19	0.07	0.1	0.1	0.1	0.19	0.1	0.11
<b>PSI</b>	<b>0.22</b>	<b>0.133</b>	<b>0.16</b>	<b>0.19</b>	<b>0.19</b>	<b>0.44</b>	<b>0.56</b>	<b>0.19</b>	<b>0.33</b>	<b>0.22</b>	<b>0.56</b>	<b>0.89</b>	<b>0.22</b>	<b>0.56</b>	<b>0.25</b>	<b>0.22</b>	<b>0.15</b>	<b>0.33</b>	<b>0.15</b>	<b>0.15</b>	<b>0.15</b>	<b>0.15</b>	<b>0.15</b>	<b>0.09</b>
599/658	0.5	0.25	0.25	0.33	0.25	0.2	0.33	0.67	0.33	0.33	0.5	0.5	0.5	0.5	0.25	0.5	0.25	0.5	0.5	0.33	0.25			
599/677	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1			
599/697	1	1	1	1	1	0.6	1	1	1	1	0.6	1	1	1	0.6	1	1	0.6	1	0.6	0.6			
599/858	0.06	0.06	0.06	0.11	0.06	0.07	0.11	0.11	0.11	0.11	0.1	0.06	0.25	0.06	0.1	0.25	0.06	0.1	0.25	0.19	0.1			
599/898	<b>0.44</b>	<b>0.19</b>	<b>0.19</b>	<b>0.22</b>	<b>0.19</b>	<b>0.13</b>	<b>0.22</b>	<b>0.56</b>	<b>0.22</b>	<b>0.22</b>	<b>0.4</b>	<b>0.44</b>	<b>0.25</b>	<b>0.44</b>	<b>0.15</b>	<b>0.25</b>	<b>0.19</b>	<b>0.4</b>	<b>0.25</b>	<b>0.15</b>	<b>0.15</b>			
658/677																								
658/697																								
658/858																								
658/898																								
658/918																								
677/697																								
677/858																								
677/898																								
677/918																								
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697/898																								
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858/898																								
858/918																								
898/918																								

- *M. bechsteinii* (Pecqueuse, FD de Rambouillet, juin 2006).

	738/558	738/578	738/778.2	558/578	558/778.2	578/778.2
OSP	0.67	1	0.33333	1	0	0
Bat1						
roosts/day	1.33	1.33	1.33	0.33	0.33	0.33
Bat2						
roosts/day	0.33	0.33	0.25	0.33	0.25	0.25
ESP	0.25	0.57	0.33417	2.296	1.3468	1.347
<b>PSI</b>	<b>0.41</b>	<b>0.43</b>	<b>-0.0008</b>	<b>-1.296</b>	<b>-1.347</b>	<b>-1.347</b>

- *M. bechsteinii* (Pecqueuse, FD de Rambouillet, août 2006).

	977/597	977/940	977/958	977/917	597/940	597/958	597/917	940/958	940/917	958/917
OSP	0.33	0	0.33	0.7	0.25	0.33	0.33	0	0	0.5
Bat1										
roosts/day	1.4	1.4	1.4	1.4	0.75	0.75	0.75	1	1	0.75
Bat2										
roosts/day	0.75	1	0.75	0.8	1	0.75	0.8	0.75	0.8	0.8
ESP	0.11	0.079	0.11	0.1	0.08	0.2	0.19	0.148	0.139	0.1
<b>PSI</b>	<b>0.23</b>	<b>-0.08</b>	<b>0.23</b>	<b>0.6</b>	<b>0.17</b>	<b>0.14</b>	<b>0.15</b>	<b>-0.15</b>	<b>-0.14</b>	<b>0.4</b>

- *M. bechsteinii* (Pecqueuse, FD de Rambouillet, août 2007).

	337/118	337/158	337/138	118/158	118/138	158/138
OSP	1	0.5	0.67	0.5	0.67	0
Bat1						
roosts/day	0.67	0.67	0.67	1	1	2
Bat2						
roosts/day	1	2	1	2	1	1
ESP	0.17	0.19	0.17	0.13	0.11	0.125
<b>PSI</b>	<b>0.83</b>	<b>0.31</b>	<b>0.5</b>	<b>0.38</b>	<b>0.56</b>	<b>-0.13</b>



- *M. bechsteinii* (Pecqueuse, FD de Rambouillet, août 2009).

	338/478	338/558	338/638	338/738	338/978	478/558	478/638	478/738	478/978	558/638	558/738	558/978	638/738	638/978	738/978
OSP	0.67	0.17	0.33	0.33	0.4	0.33	0.43	0.5	0.4	0.33	0.83	0.2	0.57	0.2	0.2
Bat1															
roosts/day	0.67	0.67	0.67	0.67	0.67	0.5	0.5	0.5	0.5	0.5	0.5	0.5	0.57	0.57	0.57
Bat2															
roosts/day	0.5	0.5	0.57	0.57	0.6	0.5	0.57	0.57	0.6	0.57	0.57	0.6	0.57	0.6	0.6
ESP	0.08	0.08	0.07	0.07	0.1	0.11	0.07	0.05	0.13	0.1	0.1	0.13	0.06	0.12	0.12
<b>PSI</b>	<b>0.58</b>	<b>0.08</b>	<b>0.26</b>	<b>0.26</b>	<b>0.3</b>	<b>0.22</b>	<b>0.36</b>	<b>0.45</b>	<b>0.27</b>	<b>0.24</b>	<b>0.74</b>	<b>0.07</b>	<b>0.51</b>	<b>0.08</b>	<b>0.08</b>

- *P. auritus* (Pecqueuse, FD de Rambouillet, juillet 2009).

	716/756	716/578	716/017	716/038	716/058	716/077	716/197	756/578	756/017	578/017	578/038	578/058	578/077	578/197	038/058	038/077	038/197	058/077	058/197	077/197
OSP	0	0	0	0	0	0	0	0.33	0	0	0	0	0	0	0	0	0.67	0	0	0
Bat1																				
roosts/day	0.33	0.33	0.33	0.33	0.33	0.33	0.33	1	1	1	1	1	1	1	1.33	1.33	1.33	0.5	0.5	1
Bat2																				
roosts/day	1	1	1	1.33	0.5	1	1	1	1	1	1.33	0.5	1	1	0.5	1	1	1	1	1
ESP	0.19	0.19	0.76	2.28	6.06	3.03	3.03	0.11	1	1	0.75	2	1	1	0.17	0.75	0.08	2	0.13	1
<b>PSI</b>	<b>-0.2</b>	<b>-0.2</b>	<b>-0.8</b>	<b>-2.3</b>	<b>-6.1</b>	<b>-3</b>	<b>-3</b>	<b>0.22</b>	<b>-1</b>	<b>-1</b>	<b>-0.8</b>	<b>-2</b>	<b>-1</b>	<b>-1</b>	<b>-0.2</b>	<b>-0.8</b>	<b>0.58</b>	<b>-2</b>	<b>-0.1</b>	<b>-1</b>

- *P. auritus* (Pecqueuse, FD de Rambouillet, août 2009).

	398/618	398/798	398/838	398/938	618/798	618/838	618/938	798/838	798/938	838/938
OSP	0.25	0	0.25	0	0	0.4	0	0	0	0
Bat1										
roosts/day	0.6	0.6	0.6	0.6	0.6	0.6	0.6	1	1	0.4
Bat2										
roosts/day	0.6	1	0.4	1	1	0.4	1	0.4	1	1
ESP	0.17	0.417	0.26	1.67	0.19	0.17	1.67	0.28	1	2.5
<b>PSI</b>	<b>0.08</b>	<b>-0.42</b>	<b>-0.01</b>	<b>-1.7</b>	<b>-0.2</b>	<b>0.23</b>	<b>-1.7</b>	<b>-0.3</b>	<b>-1</b>	<b>-2.5</b>

- *P. auritus* (Saloup, FD de Tronçais, mai 2007).

	179/199	179/299	179/379	179/399	199/299	199/379	199/399	299/379	299/399	379/399
OSP	0.67	0.5	0.5	0.83	1	0.5	0.5	0.33	0.5	0.5
Bat1 roosts/day	1	1	1	1	0.75	0.75	0.75	0.67	0.67	0.67
Bat2 roosts/day	0.75	0.67	0.67	0.67	0.67	0.67	0.67	0.67	0.67	0.67
ESP	0.15	0.04	0.04	0.04	0.12	0.12	0.12	0.06	0.06	0.06
<b>PSI</b>	<b>0.52</b>	<b>0.46</b>	<b>0.46</b>	<b>0.79</b>	<b>0.88</b>	<b>0.38</b>	<b>0.38</b>	<b>0.27</b>	<b>0.44</b>	<b>0.44</b>

- *M. bechsteinii* (Saloup, FD de Tronçais, juillet 2008).

	518/498	518/478	518/438	518/838	518/738	498/478	498/438	498/838	498/738	478/438	478/838	478/738	438/838	438/738	838/738
OSP	1	1	1	0	1	1	1	0	1	1	0	1	0	0.5	0
Bat1 roosts/day	1	1	1	1	1	1	1	1	1	1	1	1	0.75	0.75	0.67
Bat2 roosts/day	1	1	0.75	1	0.67	1	0.75	1	0.67	0.75	1	0.67	1	0.67	1
ESP	0.25	0.25	0.15	1	1.49	0.25	0.33	1	1.49	0.33	1	1.49	0.33	0.5	0.37
<b>PSI</b>	<b>0.75</b>	<b>0.75</b>	<b>0.85</b>	<b>-1</b>	<b>-0.5</b>	<b>0.75</b>	<b>0.67</b>	<b>-1</b>	<b>-0.5</b>	<b>0.67</b>	<b>-1</b>	<b>-0.5</b>	<b>-0.3</b>	<b>0</b>	<b>-0.4</b>

- *P. auritus* (Vernigeole, FD de Tronçais, août 2007).

	438/378	438/278	438/098	438/058	378/278	378/098	378/058	278/098	278/058	098/058
OSP	0.8	1	0.8	0.5	1	1	0.5	1	0.5	0.5
Bat1 roosts/day	0.8	0.8	0.8	0.8	0.6	0.6	0.6	0.8	0.8	0.6
Bat2 roosts/day	0.6	0.8	0.6	1	0.8	0.6	1	0.6	1	1
ESP	0.08	0.06	0.08	0.31	0.08	0.11	0.42	0.08	0.31	0.42
<b>PSI</b>	<b>0.72</b>	<b>0.94</b>	<b>0.72</b>	<b>0.19</b>	<b>0.92</b>	<b>0.89</b>	<b>0.08</b>	<b>0.92</b>	<b>0.19</b>	<b>0.08</b>

- *P. auritus* (Vernigeole, FD de Tronçais, août 2008).

	977/797	977/697	977/657	977/577	977/537	797/697	797/657	797/577	797/537	697/657	697/577	697/537	657/577	657/537	577/537
OSP	1	1	1	0.8	1	1	1	0.75	1	1	0.75	1	0.67	1	0.8
Bat1 roosts/day	0.8	0.8	0.8	0.8	0.8	0.75	0.75	0.75	0.75	0.75	0.75	0.75	1.33	1.33	1.4
Bat2 roosts/day	0.75	0.75	1.33	1.4	0.8	0.75	1.33	1.4	0.8	1.33	1.4	0.8	1.4	0.8	0.8
ESP	0.1	0.1	0.1	0.04	0.06	0.11	0.11	0.06	0.1	0.11	0.06	0.1	0.06	0.1	0.04
<b>PSI</b>	<b>0.9</b>	<b>0.9</b>	<b>0.9</b>	<b>0.76</b>	<b>0.94</b>	<b>0.89</b>	<b>0.89</b>	<b>0.69</b>	<b>0.9</b>	<b>0.89</b>	<b>0.69</b>	<b>0.9</b>	<b>0.61</b>	<b>0.9</b>	<b>0.76</b>

- *M. bechsteinii* (Le Plaix, FD de Tronçais, août 2008).

	618/718	618/758	618/778	618/818	618/858	618/898	618/918	718/758	718/778	718/818	718/858	718/898	718/918	758/778	758/818	758/858	758/898	758/918	778/818	778/858	778/898	778/918	818/858	818/898	818/918	858/898	858/918	898/918
OSP	0.33	0.2	0.75	0.75	0.8	0.67	0.33	0.67	0.33	0.33	0.33	0.33	0.33	0.25	0.25	0.2	0.33	0.33	1	1	0.67	0.33	1	0.67	0.33	0.67	0.33	0.33
Bat1 roosts/day	0.6	0.6	0.6	0.6	0.6	0.6	0.6	1.33	1.33	1.33	1.33	1.33	1.33	0.4	0.4	0.4	0.4	0.4	1	1	1	1	0.75	0.75	0.75	0.6	0.6	1
Bat2 roosts/day	1.33	0.4	1	0.75	0.6	1	1	0.4	1	0.75	0.6	1	1	1	0.75	0.6	1	1	0.75	0.6	1	1	0.6	1	1	1	1	1
ESP	0.14	0.17	0.1	0.14	0.11	0.19	0.19	0.21	0.08	0.11	0.14	0.08	0.08	0.16	0.21	0.17	0.28	0.28	0.08	0.1	0.11	0.11	0.14	0.15	0.15	0.19	0.19	0.11
<b>PSI</b>	<b>0.19</b>	<b>0.03</b>	<b>0.65</b>	<b>0.61</b>	<b>0.69</b>	<b>0.48</b>	<b>0.15</b>	<b>0.46</b>	<b>0.25</b>	<b>0.22</b>	<b>0.19</b>	<b>0.25</b>	<b>0.25</b>	<b>0.09</b>	<b>0.04</b>	<b>0.03</b>	<b>0.06</b>	<b>0.06</b>	<b>0.92</b>	<b>0.9</b>	<b>0.56</b>	<b>0.22</b>	<b>0.86</b>	<b>0.52</b>	<b>0.19</b>	<b>0.48</b>	<b>0.15</b>	<b>0.22</b>

- *P. auritus* (Charmoie, FD de Rambouillet, mai 2009).

	037/055	037/355	037/857	037/897	037/977	055/355	055/857	055/897	055/977	355/857	355/897	355/977	857/897	857/977	897/977
OSP	0.167	0	0.17	0.17	0	0.5	0.5	0.833	0	0	0	0	0.67	0.17	0.167
Bat1 roosts/day	1	1	1	1	1	0.43	0.43	0.43	0.43	1	1	1	0.67	0.67	0.33
Bat2 roosts/day	0.43	1	0.67	0.33	0.5	1	0.67	0.33	0.5	0.67	0.33	0.5	0.33	0.5	0.5
ESP	0.065	1	0.04	0.08	0.06	0.58	0.096	0.196	0.13	1.49	3.03	2	0.13	0.08	0.168
<b>PSI</b>	<b>0.102</b>	<b>-1</b>	<b>0.13</b>	<b>0.08</b>	<b>-0.06</b>	<b>-0.08</b>	<b>0.404</b>	<b>0.638</b>	<b>-0.13</b>	<b>-1.49</b>	<b>-3.03</b>	<b>-2</b>	<b>0.54</b>	<b>0.08</b>	<b>-0.002</b>

## Annexe 6 (Chapitre 2) : Tableau récapitulatif des valeurs d'ISI, d'IS, d'IRG, de jour/gîte et de gîtes/jour pour chaque individu suivi lors de notre étude.

Pour chaque animal est indiqué le numéro de l'individu (identifiant individuel), l'espèce, le sexe (entre M et F), l'Age (entre Juv et A), l'année, le mois, l'avant-bras et le poids de l'animal, l'état sexuel (entre sexuellement non actif SNA, GES pour gestante et ALL pour allaitante). Sont ensuite indiquées les valeurs de P (nb moyen quotidien de partenaires potentiels de gîte disponibles pour le partage), de Ind (nb d'individus suivis avec lesquels un individu donné partage un gîte), l'ISI, GI (nb gîtes de l'individu), le nombre de jours de suivi, le nombre de changements de gîtes observés lors du suivi (il est arrivé qu'un individu change de gîte tous les jours, mais en alternant entre seulement 2 ou 3 gîtes), jour/gîte, roost/day, le nb de jours avec au moins un partenaire, IS, GR (parmi les gîtes de l'individu suivi, nb gîtes réutilisés par d'autres individus équipés) et enfin IRG.

N° individu	Espèce	Sexe	Age	Année	Mois	AB	Poids	Etat sexuel	P	Ind	ISI	GI	nb jours de suivis	changements de gîtes	jour/gîte	gîtes/jour	nb de j avec au moins 1 partenaire	IS	GR	IRG
1Mbe2006-2-F-A-558	Mbe	F	A	2006	07	43.8	11	ALL	2.67	4	<b>0.5</b>	1	3	1	3	0.333	2	<b>0.67</b>	1	<b>1</b>
1Mbe2006-2-F-A-578	Mbe	F	A	2006	06	41.2	9.7	ALL	2.33	4	<b>0.571</b>	1	3	1	3	0.333	2	<b>0.67</b>	1	<b>1</b>
1Mbe2006-2-F-A-738	Mbe	F	A	2006	07	42.5	11	GES	2.67	5	<b>0.625</b>	4	3	3	1	1.333	3	<b>1</b>	2	<b>0.67</b>
1Mbe2006-2-F-A-778.2	Mbe	F	A	2006	06	39.5	9.2	ALL	2.25	1	<b>0.111</b>	1	4	1	4	0.25	1	<b>0.25</b>	1	<b>1</b>
1Mbe2006-3-F-A-917	Mbe	F	A	2006	08	40.1	10	ALL	3.25	5	<b>0.308</b>	4	5	4	1.25	0.8	2	<b>0.4</b>	3	<b>0.75</b>
1Mbe2006-3-F-A-958	Mbe	F	A	2006	08	43	10	SNA	3.25	4	<b>0.308</b>	3	4	4	1	0.75	1	<b>0.25</b>	3	<b>1</b>
1Mbe2006-3-F-A-977	Mbe	F	A	2006	08	42	9.8	SNA	3	4	<b>0.267</b>	7	5	5	1	1.4	3	<b>0.6</b>	3	<b>0.43</b>
1Mbe2006-3-F-J-940	Mbe	F	Juv	2006	08	41.5	9.9	SNA	3.25	1	<b>0.077</b>	4	4	4	1	1	1	<b>0.25</b>	3	<b>0.75</b>
1Mbe2006-3-M-J-597	Mbe	M	Juv	2006	08	41	9	SNA	3.25	4	<b>0.308</b>	3	4	3	1.33	0.75	3	<b>0.75</b>	2	<b>0.67</b>
1Mbe2007-3-F-A-118	Mbe	F	A	2007	08	47	9.3	ALL	2.67	6	<b>0.75</b>	3	3	3	1	1	3	<b>1</b>	2	<b>0.67</b>
1Mbe2007-3-F-A-138	Mbe	F	A	2007	08	43	9.8	ALL	2.67	4	<b>0.5</b>	3	3	3	1	1	2	<b>0.67</b>	2	<b>0.67</b>
1Mbe2007-3-F-A-158	Mbe	F	A	2007	08	46	9.1	ALL	2	2	<b>0.5</b>	4	2	2	1	2	1	<b>0.5</b>	2	<b>0.5</b>
1Mbe2007-3-F-J-337	Mbe	F	Juv	2007	08	39.9	7.8	SNA	2.67	6	<b>0.75</b>	2	3	2	1.5	0.667	3	<b>1</b>	2	<b>1</b>
1Mbe2009-3-F-A-338	Mbe	F	A	2009	8	42,6	9,9	SNA	4.83	11	<b>0.379</b>	4	6	4	1.5	0.667	4	<b>0.67</b>	2	<b>0.5</b>
1Mbe2009-3-F-A-478	Mbe	F	A	2009	8	41,7	9,2	SNA	4	15	<b>0.469</b>	4	8	6	1.33	0.5	6	<b>0.75</b>	4	<b>1</b>
1Mbe2009-3-F-A-738	Mbe	F	A	2009	8	44,5	11	ALL	4	16	<b>0.5</b>	4	8	5	1.6	0.5	7	<b>0.88</b>	4	<b>1</b>
1Mbe2009-3-F-J-558	Mbe	F	Juv	2009	8	42,9	9,2	SNA	4.83	11	<b>0.379</b>	3	6	4	1.5	0.5	5	<b>0.83</b>	3	<b>1</b>
1Mbe2009-3-F-J-638	Mbe	F	Juv	2009	8	42,1	9,7	SNA	4.43	12	<b>0.387</b>	4	7	4	1.75	0.571	4	<b>0.57</b>	3	<b>0.75</b>
1Mbe2009-3-F-J-978	Mbe	F	Juv	2009	8	42,3	9,1	SNA	5	7	<b>0.28</b>	3	5	3	1.67	0.6	2	<b>0.4</b>	3	<b>1</b>
1Mna2009-2-F-A-119	Mna	F	A	2009	7	41,1	9,4	ALL	4.67	6	<b>0.429</b>	2	3	1	3	0.33	2	<b>0.67</b>	2	<b>1</b>
1Mna2009-2-F-A-139	Mna	F	A	2009	7	40,2	8,5	ALL	5	5	<b>0.5</b>	2	2	2	1	1	1	<b>0.5</b>	1	<b>0.5</b>
1Mna2009-2-F-A-158	Mna	F	A	2009	7	38,4	8	ALL	4	8	<b>0.667</b>	2	3	2	1.5	0.67	3	<b>1</b>	2	<b>1</b>
1Mna2009-2-F-A-179	Mna	F	A	2009	7	40,1	9,2	ALL	4	10	<b>0.625</b>	3	4	3	1.33	0.75	4	<b>1</b>	3	<b>1</b>

N° individu	Espèce	Sexe	Age	Année	Mois	AB	Poids	Etat sexuel	P	Ind	ISI	GI	nb jours de suivis	changements de gîtes	jour/gîte	gîtes/jour	nb de j avec au moins 1 partenaire	IS	GR	IRG
1Mna2009-3-F-A-697	Mna	F	A	2009	8	40,8	8,8	ALL	8	14	<b>0.438</b>	4	4	4	1	1	4	<b>1</b>	4	<b>1</b>
1Mna2009-2-F-A-219	Mna	F	A	2009	7	39,8	8,4	ALL	4.67	8	<b>0.429</b>	2	4	2	2	0.5	3	<b>0.75</b>	2	<b>1</b>
1Mna2009-2-F-A-238	Mna	F	A	2009	7	39,6	8,7	ALL	4.67	7	<b>0.5</b>	3	3	3	1	1	2	<b>0.67</b>	2	<b>0.67</b>
1Mna2009-2-F-A-398	Mna	F	A	2009	7	37,5	7,4	ALL	4	2	<b>0.083</b>	3	6	3	2	0.5	0	<b>0</b>	0	<b>0</b>
1Mna2009-3-F-A-858	Mna	F	A	2009	8	40,3	8,7	SNA	7.67	10	<b>0.435</b>	3	3	3	1	1	2	<b>0.67</b>	2	<b>0.67</b>
1Mna2009-3-F-J-418	Mna	F	Juv	2009	8	39,8	7,3	SNA	7.4	12	<b>0.324</b>	5	5	5	1	1	3	<b>0.6</b>	3	<b>0.6</b>
1Mna2009-3-F-J-458	Mna	F	Juv	2009	8	39,4	7,4	SNA	8.67	13	<b>0.5</b>	3	3	3	1	1	3	<b>1</b>	3	<b>1</b>
1Mna2009-3-F-J-497	Mna	F	Juv	2009	8	40,8	7,9	SNA	7.4	10	<b>0.27</b>	3	5	3	1.67	0.6	2	<b>0.4</b>	2	<b>0.67</b>
1Mna2009-3-F-J-599	Mna	F	Juv	2009	8	37,1	6,8	SNA	7.4	12	<b>0.324</b>	5	5	5	1	1	3	<b>0.6</b>	4	<b>0.8</b>
1Mna2009-3-F-J-658	Mna	F	Juv	2009	8	39,7	7,5	SNA	7.5	14	<b>0.467</b>	4	4	4	1	1	4	<b>1</b>	4	<b>1</b>
1Mna2009-3-F-J-677	Mna	F	Juv	2009	8	42	7,7	SNA	8	11	<b>0.344</b>	4	4	4	1	1	3	<b>0.75</b>	4	<b>1</b>
1Mna2009-3-F-J-898	Mna	F	Juv	2009	8	40,9	7,95	SNA	8	10	<b>0.313</b>	4	4	4	1	1	2	<b>0.5</b>	2	<b>0.5</b>
1Mna2009-3-F-J-918	Mna	F	Juv	2009	8	38,2	7,1	SNA	7.4	12	<b>0.324</b>	3	5	4	1.25	0.6	3	<b>0.6</b>	3	<b>1</b>
1Paur2007-1-F-A-058	Paur	F	A	2007	04	38	6,5	GES	1	0	<b>0</b>	3	9	3	3	0.333	0	<b>0</b>	1	<b>0.33</b>
1Paur2007-1-F-A-078	Paur	F	A	2007	04	38,3	6,95	GES	1	0	<b>0</b>	4	8	4	2	0.5	0	<b>0</b>	1	<b>0.25</b>
1Paur2009-1-F-A-055	Paur	F	A	2009	4	38,3	8,1	SNA	4.33	10	<b>0.33</b>	3	7	3	2.33	0.429	5	<b>0.71</b>	1	<b>0.33</b>
1Paur2009-1-F-A-355	Paur	F	A	2009	4	40,8	8,3	SNA	3	1	<b>0.167</b>	2	2	2	1	1	1	<b>0.5</b>	2	<b>1</b>
1Paur2009-1-F-A-897	Paur	F	A	2009	4	40	8,3	NA	4.17	11	<b>0.44</b>	2	6	2	3	0.333	6	<b>1</b>	2	<b>1</b>
1Paur2009-1-F-A-977	Paur	F	A	2009	4	37,5	7,6	NA	4.17	2	<b>0.08</b>	3	6	3	2	0.5	1	<b>0.17</b>	1	<b>0.33</b>
1Paur2009-1-M-A-037	Paur	M	A	2009	4	39,4	9,3	SNA	4.17	3	<b>0.12</b>	6	6	6	1	1	1	<b>0.17</b>	1	<b>0.17</b>
1Paur2009-1-M-A-857	Paur	M	A	2009	4	38,8	7,3	SNA	4.17	9	<b>0.36</b>	4	6	4	1.5	0.667	4	<b>0.67</b>	2	<b>0.5</b>
1Paur2009-2-F-A-038	Paur	F	A	2009	7	39,2	8,7	ALL	3	2	<b>0.222</b>	4	3	3	1	1.333	2	<b>0.67</b>	3	<b>0.75</b>
1Paur2009-2-F-A-058	Paur	F	A	2009	7	41,8	9,8	ALL	2.5	1	<b>0.1</b>	2	4	2	2	0.5	1	<b>0.25</b>	1	<b>0.5</b>
1Paur2009-2-F-A-077	Paur	F	A	2009	7	38,9	7,6	GES	5	1	<b>0.2</b>	1	1	1	1	1	1	<b>1</b>	1	<b>1</b>
1Paur2009-2-F-A-197	Paur	F	A	2009	7	37,8	11	ALL	1.67	2	<b>0.4</b>	3	3	3	1	1	2	<b>0.67</b>	3	<b>1</b>
1Paur2009-2-F-A-716	Paur	F	A	2009	6	39,5	7,9	ALL	3.25	0	<b>0</b>	2	6	2	3	0.333	0	<b>0</b>	0	<b>0</b>
1Paur2009-2-M-A-017	Paur	M	A	2009	7	37,2	8	SNA	3	0	<b>0</b>	2	2	2	1	1	0	<b>0</b>	0	<b>0</b>
1Paur2009-2-M-A-578	Paur	M	A	2009	7	39,1	12	SNA	3.25	1	<b>0.077</b>	4	4	4	1	1	1	<b>0.25</b>	1	<b>0.25</b>
1Paur2009-2-M-A-756	Paur	M	A	2009	7	38,5	5,9	SNA	2.67	1	<b>0.125</b>	3	3	3	1	1	1	<b>0.33</b>	1	<b>0.33</b>
1Paur2009-3-F-A-838	Paur	F	A	2009	8	37,2	9	ALL	2.6	3	<b>0.231</b>	2	5	2	2.5	0.4	3	<b>0.6</b>	2	<b>1</b>
1Paur2009-3-F-J-398	Paur	F	juv	2009	8	38,7	7,2	SNA	2.75	2	<b>0.145</b>	3	5	3	1.67	0.6	2	<b>0.4</b>	1	<b>0.33</b>

N° individu	Espèce	Sexe	Age	Année	Mois	AB	Poids	Etat sexuel	P	Ind	ISI	GI	nb jours de suivis	changements de gîtes	jour/gîte	gîtes/jour	nb de j avec au moins 1 partenaire	IS	GR	IRG
1Paur2009-3-F-J-938	Paur	F	juv	2009	8	38,6	7	SNA	4	0	0	2	1	1	1	1	0	0	0	0
1Paur2009-3-F-PJ-618	Paur	F	1an	2009	8	40,8	9,2	ALL	2.6	3	0.231	3	5	5	1	0.6	3	0.6	2	0.67
1Paur2009-3-M-J-798	Paur	M	juv	2009	8	37,7	7,5	SNA	3	0	0	3	3	3	1	1	0	0	1	0.33
2Mbe2008-2-F-PJ-498	Mbe	F	Juv	2008	07	43.1	10.1	SNA	4	7	0.875	2	2	2	1	1	2	1	2	1
2Mbe2008-2-F-A-438	Mbe	F	A	2008	07	43.3	11.5	GES	2.75	8	0.727	3	4	4	1	0.75	3	0.75	3	1
2Mbe2008-2-F-A-478	Mbe	F	A	2008	07	40.4	8.5	SNA	4	7	0.583	3	3	3	1	1	2	0.67	3	1
2Mbe2008-2-F-A-518	Mbe	F	A	2008	07	40.5	9.3	SNA	3	8	0.889	3	3	3	1	1	3	1	3	1
2Mbe2008-2-F-A-738	Mbe	F	A	2008	07	41.2	10.5	GES	3.5	4	0.381	2	3	2	1.5	0.667	1	0.33	1	0.5
2Mbe2008-2-M-A-838	Mbe	M	A	2008	07	41.6	9	SNA	3.5	0	0	2	2	2	1	1	0	0	0	0
2Mbe2008-3-F-A-618	Mbe	F	A	2008	08	43	8.9	SNA	5.4	15	0.556	3	5	3	1.67	0.6	4	0.8	2	0.67
2Mbe2008-3-F-A-778	Mbe	F	A	2008	08	40.6	9.1	SNA	6.25	16	0.64	4	4	3	1.33	1	4	1	4	1
2Mbe2008-3-F-A-818	Mbe	F	A	2008	08	42	10	ALL	6.25	16	0.64	3	4	3	1.33	0.75	4	1	3	1
2Mbe2008-3-F-A-858	Mbe	F	A	2008	08	42.5	9.5	ALL	5.4	17	0.63	3	5	3	1.67	0.6	5	1	3	1
2Mbe2008-3-F-A-898	Mbe	F	A	2008	08	44.3	9.85	SNA	7	11	0.524	3	3	3	1	1	2	0.67	2	0.67
2Mbe2008-3-F-J-758	Mbe	F	Juv	2008	08	41.6	8.7	SNA	5.4	8	0.296	2	5	2	2.5	0.4	1	0.2	1	0.5
2Mbe2008-3-F-J-918	Mbe	F	Juv	2008	08	42.2	9.9	SNA	7	7	0.333	3	3	3	1	1	1	0.33	1	0.33
2Mbe2008-3-M-J-718	Mbe	M	Juv	2008	08	39.6	7.7	SNA	7	8	0.381	4	3	3	1	1.333	2	0.67	2	0.5
2Paur2007-1-F-A-199	Paur	F	A	2007	05	41	8.3	GES	4	10	0.625	3	4	3	1.33	0.75	4	1	3	1
2Paur2007-1-F-A-299	Paur	F	A	2007	05	40.7	8.2	SNA	3.67	12	0.545	4	6	4	1.5	0.667	5	0.83	3	0.75
2Paur2007-1-F-A-379	Paur	F	A	2007	05	39	7.9	GES	3.67	10	0.455	4	6	4	1.5	0.667	3	0.5	3	0.75
2Paur2007-1-F-A-399	Paur	F	A	2007	05	40.1	8.3	GES	3.67	13	0.591	4	6	4	1.5	0.667	5	0.83	4	1
2Paur2007-1-M-A-179	Paur	M	A	2007	05	37.2	6.9	SNA	3.67	13	0.591	6	6	5	1.2	1	5	0.83	4	0.67
2Paur2007-3-F-A-058	Paur	F	A	2007	08	38.1	6.9	SNA	4	4	0.5	2	2	2	1	1	1	0.5	1	0.5
2Paur2007-3-F-A-098	Paur	F	A	2007	08	38.5	7.15	SNA	3.4	15	0.882	3	5	3	1.67	0.6	5	1	3	1
2Paur2007-3-F-A-278	Paur	F	A	2007	08	39.4	7.8	ALL	3.4	15	0.882	4	5	4	1.25	0.8	5	1	3	0.75
2Paur2007-3-F-A-378	Paur	F	A	2007	08	37.9	7.2	ALL	3.4	15	0.882	3	5	3	1.67	0.6	5	1	3	1
2Paur2007-3-F-A-438	Paur	F	A	2007	08	38	7.1	ALL	3.4	14	0.824	4	5	3	1.67	0.8	5	1	4	1
2Paur2008-2-F-A-458	Paur	F	A	2008	07	41	12	ALL	0.5	1	0.5	2	4	2	2	0.5	1	0.25	1	0.5
2Paur2008-2-F-A-558	Paur	F	A	2008	07	39.6	8.9	SNA	0.5	1	1	1	2	1	2	0.5	1	0.5	1	1
2Paur2008-3-F-A-537	Paur	F	A	2008	08	37.7	8.1	ALL	4.2	20	0.952	4	5	3	1.67	0.8	5	1	4	1
2Paur2008-3-F-A-577	Paur	F	A	2008	08	39.5	8.1	ALL	4.2	16	0.762	7	5	4	1.25	1.4	4	0.8	4	0.57

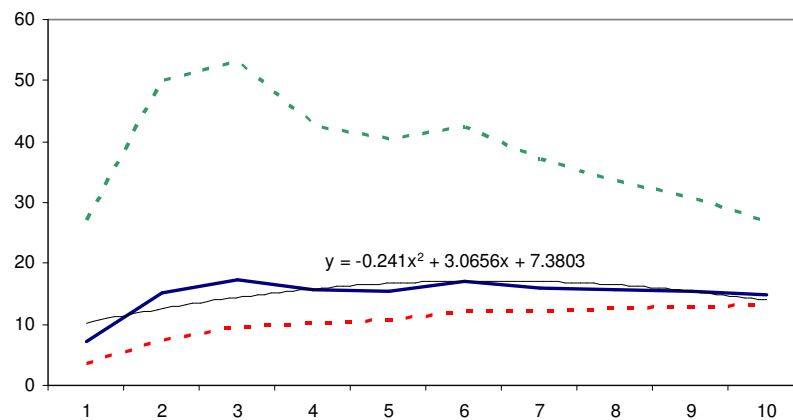
N° individu	Espèce	Sexe	Age	Année	Mois	AB	Poids	Etat sexuel	P	Ind	ISI	GI	nb jours de suivis	changements de gîtes	jour/gîte	gîtes/jour	nb de j avec au moins 1 partenaire	IS	GR	IRG
2Paur2008-3-F-A-657	Paur	F	A	2008	08	37.7	8.15	ALL	5	14	<b>0.933</b>	4	3	3	1	1.333	3	<b>1</b>	4	<b>1</b>
2Paur2008-3-F-A-797	Paur	F	A	2008	08	38.4	8.1	ALL	4.75	18	<b>0.947</b>	3	4	3	1.33	0.75	4	<b>1</b>	3	<b>1</b>
2Paur2008-3-F-A-977	Paur	F	A	2008	08	40	7.8	ALL	4.2	20	<b>0.952</b>	4	5	3	1.67	0.8	5	<b>1</b>	4	<b>1</b>
2Paur2008-3-M-A-697	Paur	M	A	2008	08	38.2	7.7	SNA	4.75	18	<b>0.947</b>	3	4	3	1.33	0.75	4	<b>1</b>	3	<b>1</b>

## Annexe 7 (Chapitre 2) : Courbes d'accumulation du nombre total de gîtes utilisés par chaque population.

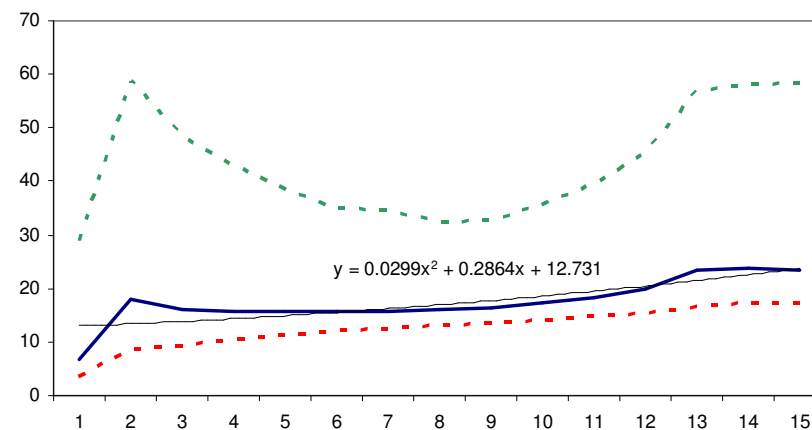
Les graphiques représentent des courbes d'accumulation calculées par CMR (méthode de Chao1, EstimateS 7.5.2) du nombre de gîtes sélectionnées par des groupes d'individus. En abscisse est représenté le nombre de chiroptères suivis par groupe. La courbe pleine (en bleu) représente la moyenne de la modélisation du nombre de cavités réellement utilisées, les courbes en pointillées représentant les courbes d'écart-type basse (en rouge) et d'écart-type haute (en vert). Enfin, la courbe en pointillés noirs représente la courbe de tendance de la courbe moyenne (polynomiale, créée dans excel), avec l'équation correspondante.

### Cas de *Plecotus auritus*

Site de Saloup (forêt de Tronçais) : Stagne à 16.94 (à partir de 6 individus), voire redescend à 15. Ce groupe utilise un relativement petit nombre de cavités.

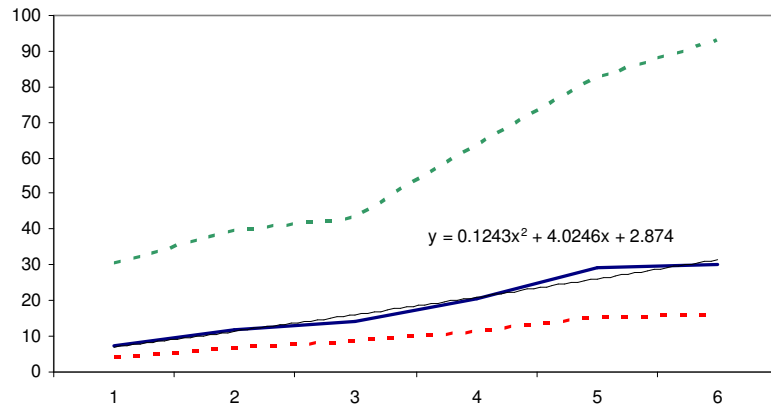


Site de la Vernigeole (forêt de Tronçais) : Plafonne à 23.81 gîtes pour les 14 individus suivis

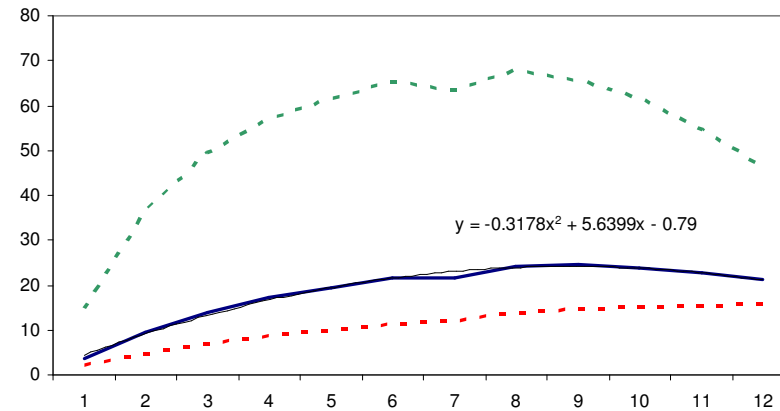




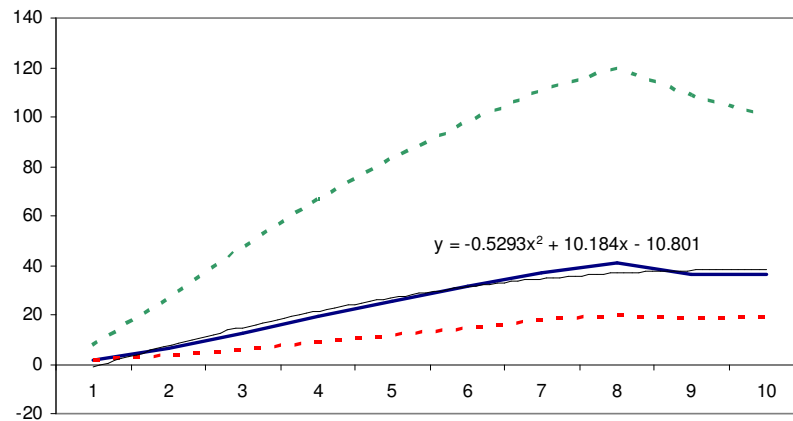
Site de la Charmoie (forêt de Rambouillet) : Progression constante, stagne à 15.98 à la fin.



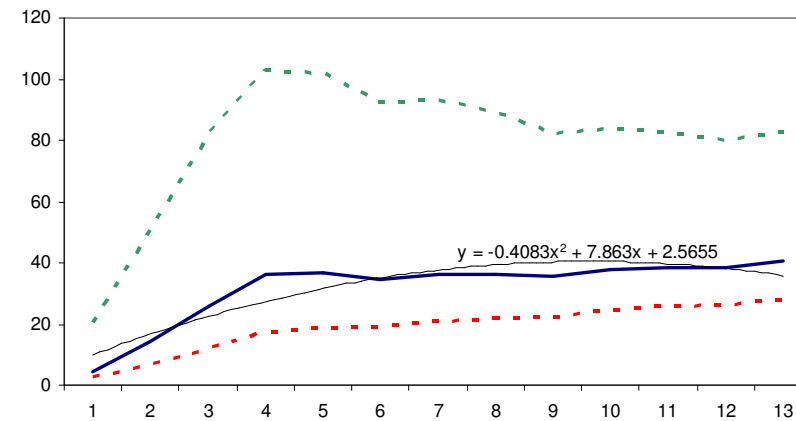
Site de l'étang Rompu (forêt de Rambouillet) : Augmente puis diminue après un plafond à 24.69. *In fine*, la courbe stoppe à 21.2 gîtes.



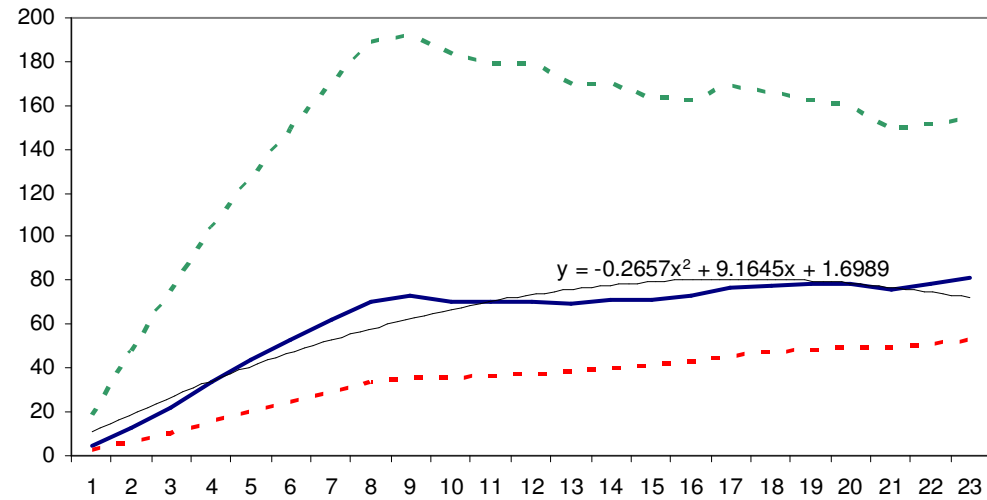
Site du Petit Etang Neuf (forêt de Rambouillet) : Augmente bien, puis monte jusqu'à 41.08 pour redescendre et se stabiliser à 36 (3 périodes de suivi). Cette stabilité traduit soit un nombre limité de cavités disponibles, soit un choix des animaux vers un nombre de 36 cavités différentes utilisées par le groupe. Compte tenu du faible effectif de la colonie (entre 10 et 20 individus probablement, obtenu par comptage en sortie de gîte), nous plaçons pour la 2<sup>nd</sup>e hypothèse.



Site de Pecqueuse (forêt de Rambouillet) : Colonie qui utilise un nombre constant de gîtes (2 périodes de suivi). Traduit une grande disponibilité, qui permet probablement à la colonie de grossir sans contrainte sur les gîtes à utiliser.

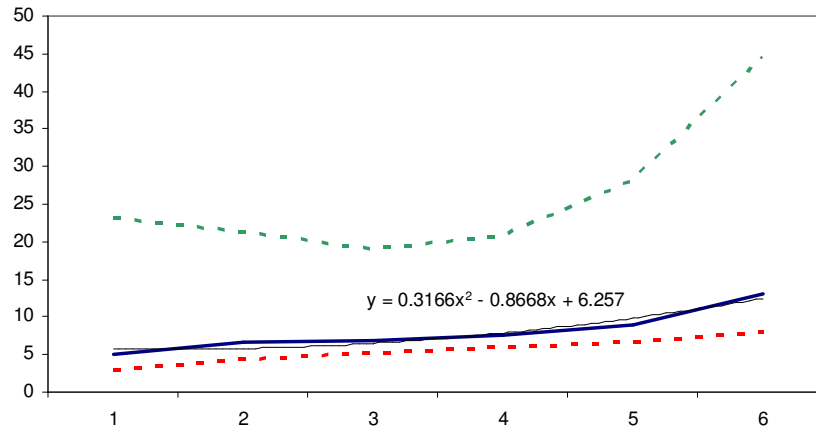


Modélisation globale pour l'ensemble des colonies proches les unes des autres (sites de Pecqueuse et du Petit Etang Neuf). La modélisation intègre de fait 2 colonies bien distinctes l'une de l'autre, et distantes de 3 km, distance d'apparence suffisante pour limiter les échanges entre les 2 colonies. Ces colonies semblent de petite taille (une dizaine d'individus à chaque fois, peut-être plus), et une utilisation permanente de nouveaux gîtes au cours du suivi, surtout le site de Pecqueuse. Ici, la courbe d'accumulation monte jusqu'à 80.88 gîtes, et ne semble pas vouloir s'arrêter, traduisant une forte disponibilité en cavités.

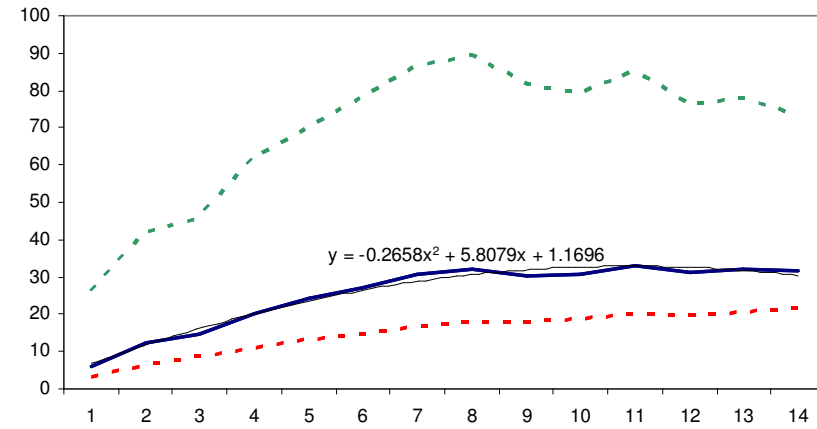


### Cas de *Myotis bechsteinii*

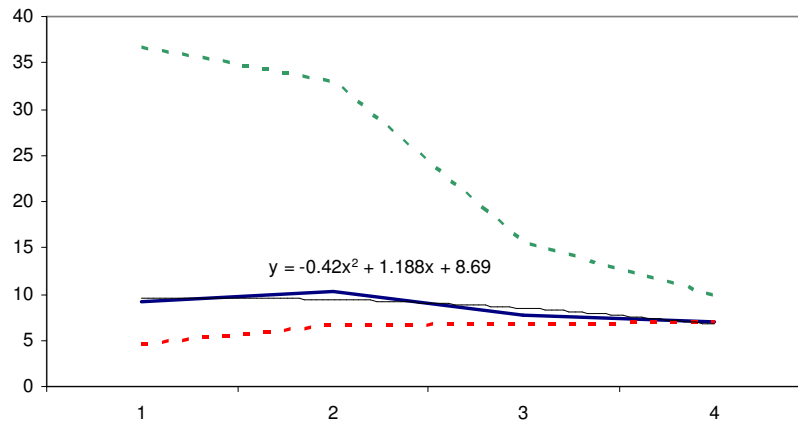
Site de Saloup (forêt de Tronçais) : En progression constante, mais correspond à un petit groupe suivi parmi une plus grosse colonie (dont l'effectif ne pouvait pas être estimé).



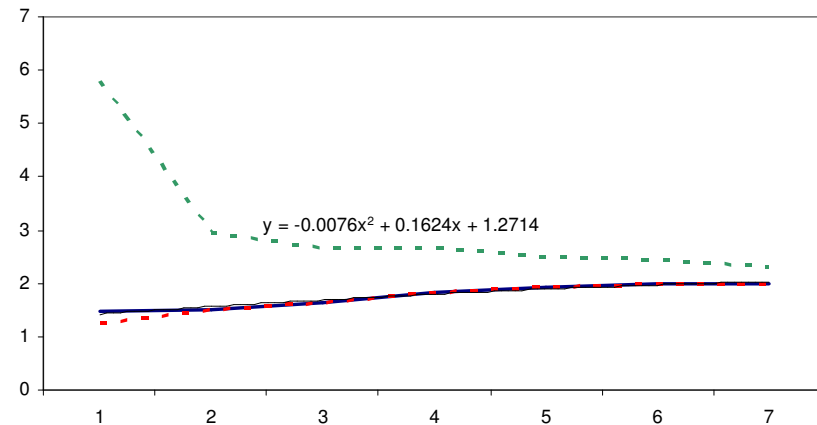
Site du Plaix (forêt de Tronçais) : Monte à 33.06 gîtes pour redescendre à 31.75 et s'y stabiliser, alors que la colonie est importante (plus de 60 à 80 femelles avant reproduction)



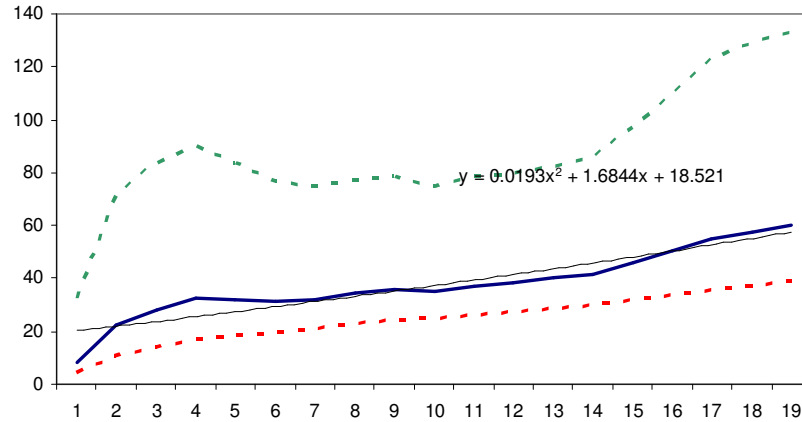
Site A (forêt de Tronçais) : Seulement 4 individus ont pu être suivis sur le long terme. Ce problème d'échantillonnage explique probablement les résultats de la modélisation.



Site B (forêt de Tronçais) : L'échantillonnage est faible, mais l'estimation reste bonne, avec seulement 2 arbres gîtes disponibles sur une grande surface prospectée (habitats : jeune forêt, entre les gaulis et les perchis de chêne).

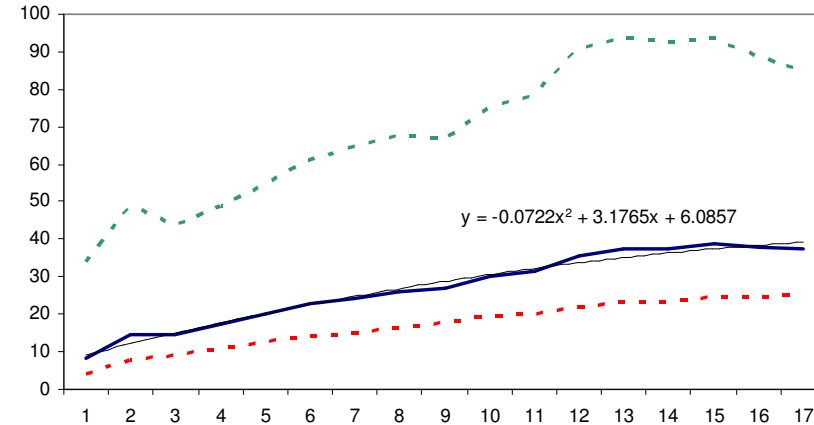


Site de Pecqueuse (forêt de Rambouillet) : On n'observe pas de plafond, le nombre de gîtes utilisés augmente toujours. Des comptages partiels en sortie de gîtes (car comptage simultanée de seulement 2 groupes) ont montré au moins 33 individus. Si on l'applique à cette courbe, cela traduit l'utilisation d'au moins 95 cavités différentes par cette méta colonie.



### Cas de *Myotis nattereri*

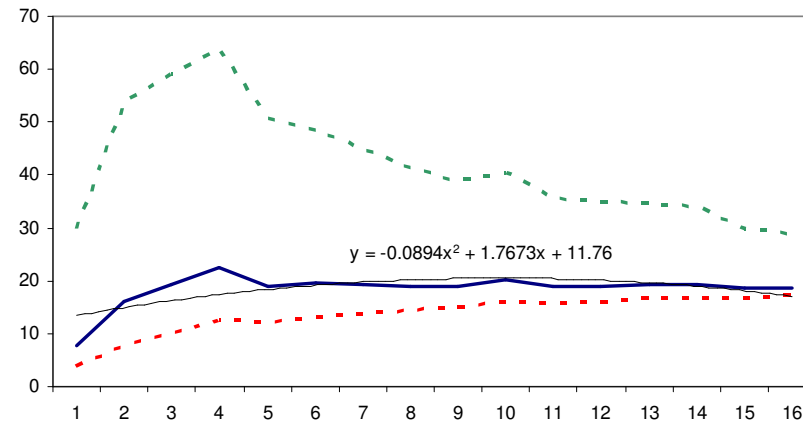
Site de Pecqueuse (forêt de Rambouillet) : La modélisation montre une augmentation constante du nombre de gîtes utilisés, puis une stagnation à 38.64.



### Les modélisation interspécifiques et intrasites.

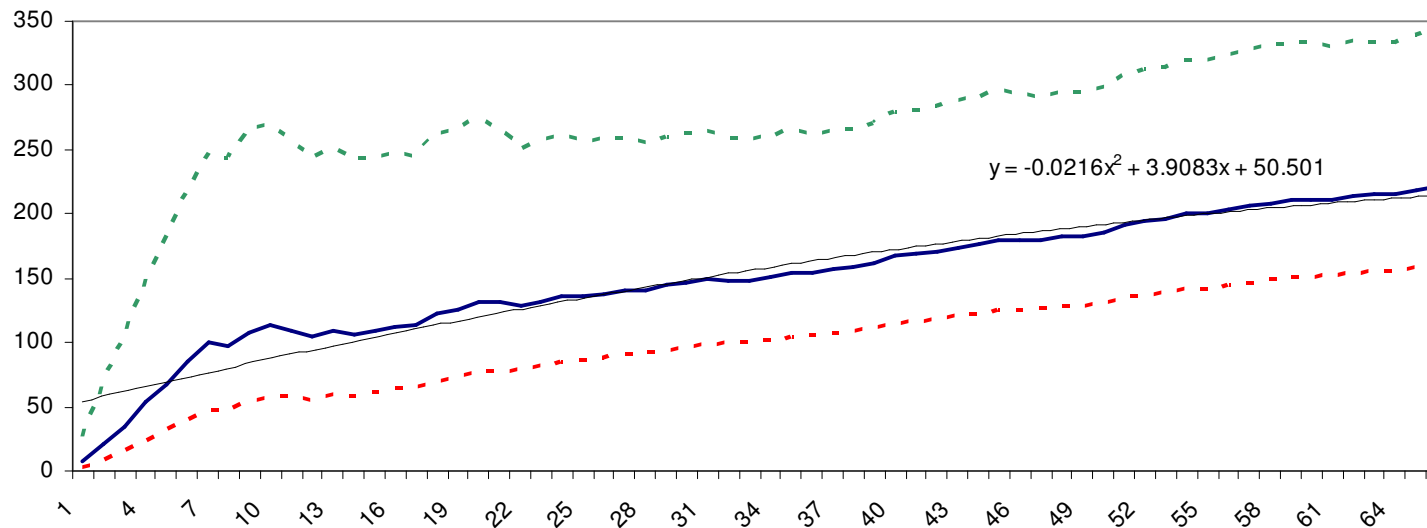
Site de Saloup (10 *Plecotus auritus* et 6 *Myotis bechsteinii*) (forêt de Tronçais).

Cette modélisation augmente dans un premier temps jusqu'à 19.28 gîtes, puis redescend à partir de 14 pour terminer à 18.67 pour les 16 individus présents. Le partage de gîtes entre les 2 espèces est en effet mis en évidence ici, avec 3 gîtes partagés entre les 2 espèces, à des moments différents, pour un total de 17 gîtes repérés pendant le suivi.



Site de Pecqueuse (19 *Myotis bechsteinii*, 17 *Myotis nattereri*, 5 *Pipistrellus pipistrellus* et 25 *Plecotus auritus*) (forêt de Rambouillet).

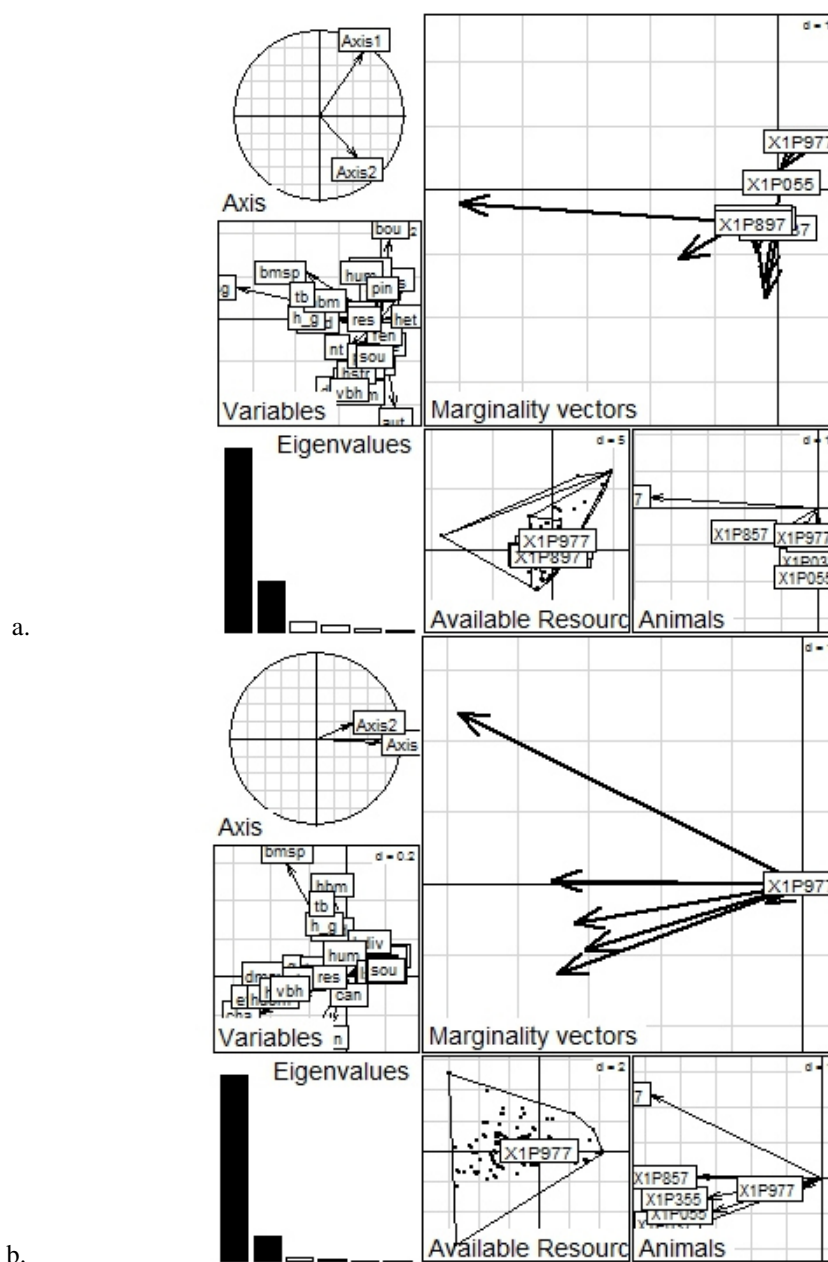
La modélisation intègre 66 individus de 4 espèces différentes. Le partage de gîtes a existé parfois pour 3 espèces, utilisant la même cavité. Nous avons par exemple observé au moins 2 *P. pipistrellus* mâles accompagnant un groupe d'au moins 5 femelles de *M. nattereri* dans la même fissure à 2m de hauteur dans un bouleau. Une autre fois, nous avons observé 10 *P. auritus* femelles dans un trou de pic en bord de chemin (juin 2006). Dans cette même cavité, une femelle de *M. bechsteinii* y est venue en août 2006, puis un mâle de *P. pipistrellus* en avril 2007. Notre modélisation montre donc une augmentation constante de l'utilisation des cavités disponibles, mettant ainsi en évidence que le nombre de cavités ne semble pas être un facteur limitant sur le site en question. Au bout des 66 individus intégrés au modèle, 221.06 cavités semblent avoir été utilisées sur la zone, toutes espèces confondues, ce qui est considérable. Et encore, nous savons que ce nombre est erroné, dans la mesure où le nombre d'individus présents sur la zone est probablement bien supérieur à 66 pour toutes ces espèces.



## Annexe 8 (Chapitre 5) : Représentation des résultats issus de la K-select sur la sélection d'habitats pour trois espèces de Chiroptères forestiers : *Myotis bechsteinii*, *M. nattereri* et *Plecotus auritus*.

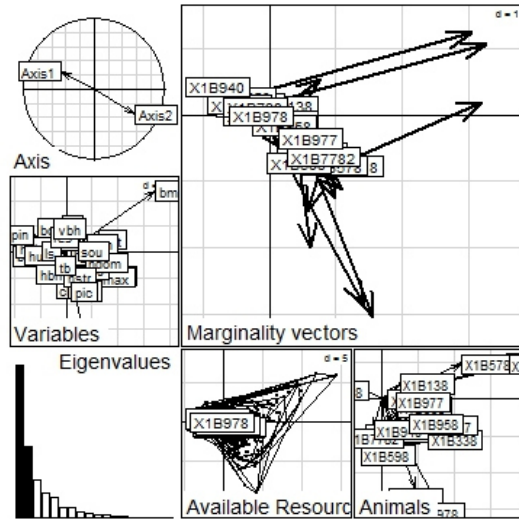
Ces résultats graphiques ont été réalisés à partir de la K-select, à l'aide du MCPb (zone tampon correspondant au h moyen, a) et du MCPb 1000 (zone tampon de 1 000 m, b). La K-select correspond à une ACP non centrée. Tous les points illustrant l'espace disponible sont centrés de façon à ce que la moyenne soit nulle, les différents individus sont positionnés dans cet espace (« available ressources »). Ces points d'espace disponible sont distribués selon différentes variables, dont les directions et les poids d'intensité varient (« Variables »). Compte-tenu de l'espace disponible, les individus sont ensuite projetés dans cet espace écologique, pour définir leur niveau de sélection (« Marginality vectors »). A chaque animal sont associés une position écologique et un vecteur de marginalité, dont la direction et l'amplitude sont représentées par une flèche. Plus un individu est éloigné du centre écologique disponible, et plus le vecteur de marginalité est important, donc plus il exerce une sélection d'habitat élevée.

- Site de la Charmoie (Forêt de Rambouillet) : *Plecotus auritus*.

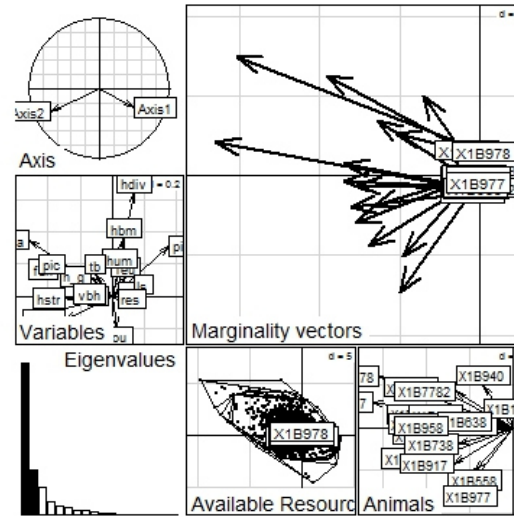


- Site de Pecqueuse (Forêt de Rambouillet) : *Myotis bechsteinii*.

a.

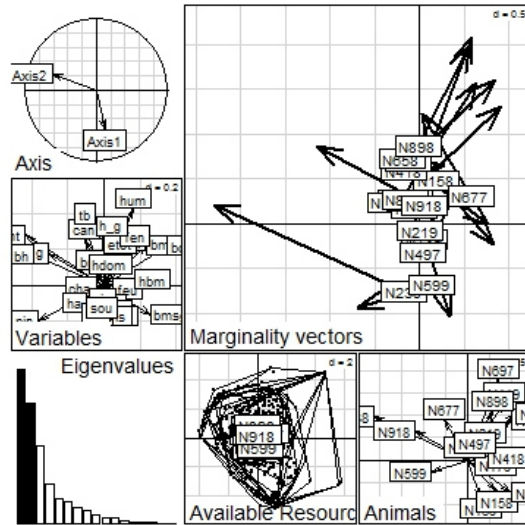


b.

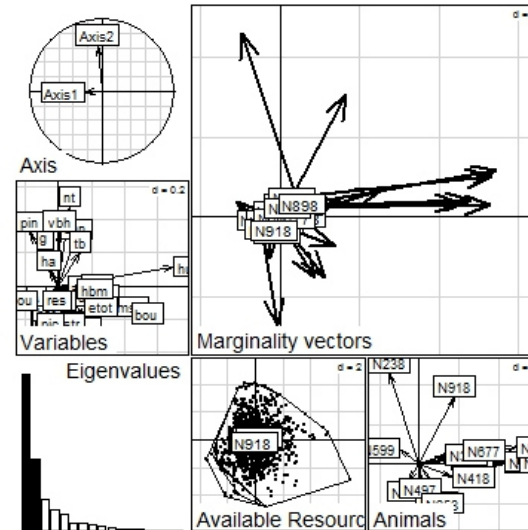


- Site de Pecqueuse (Forêt de Rambouillet) : *Myotis nattereri*.

a.

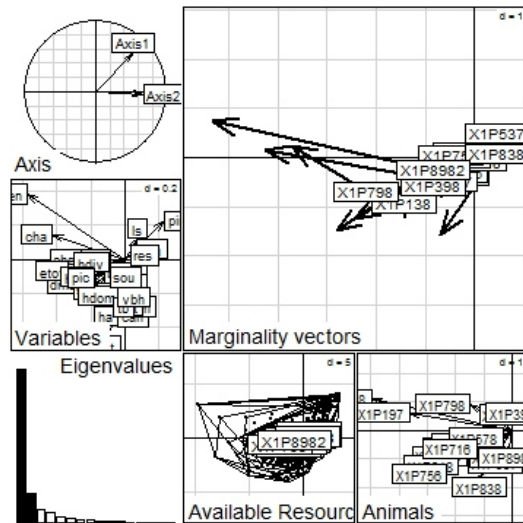


b.

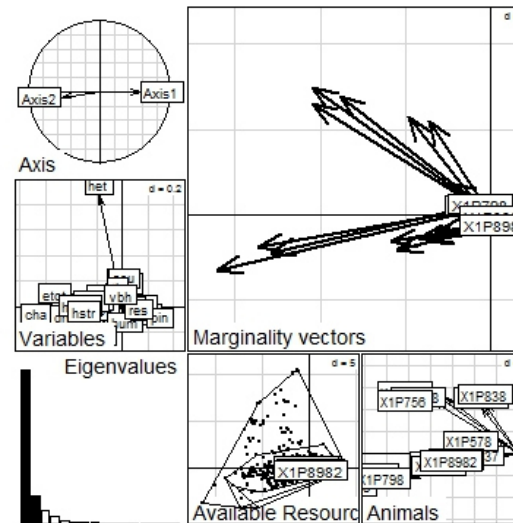


- Site de Pecqueuse (Forêt de Rambouillet) : *Plecotus auritus*.

a.

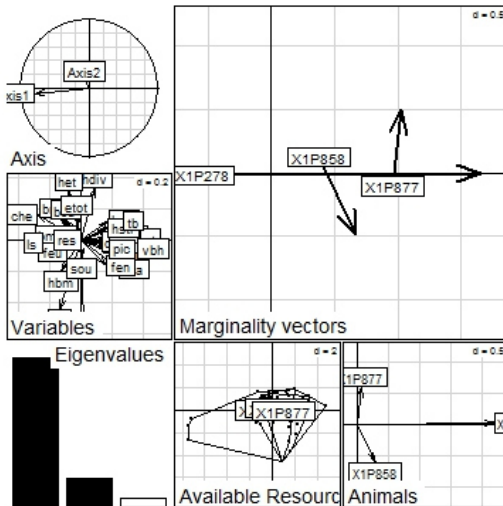


b.

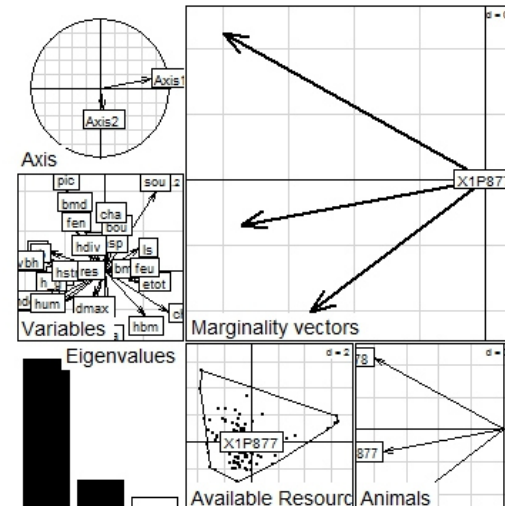


- Site de Plainvaux (Forêt de Rambouillet) : *Plecotus auritus*.

a.



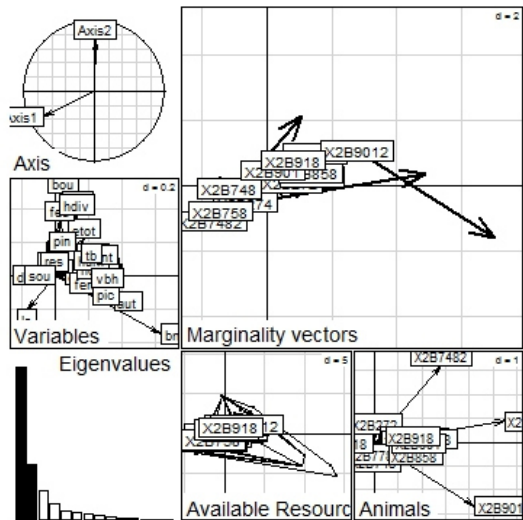
b.



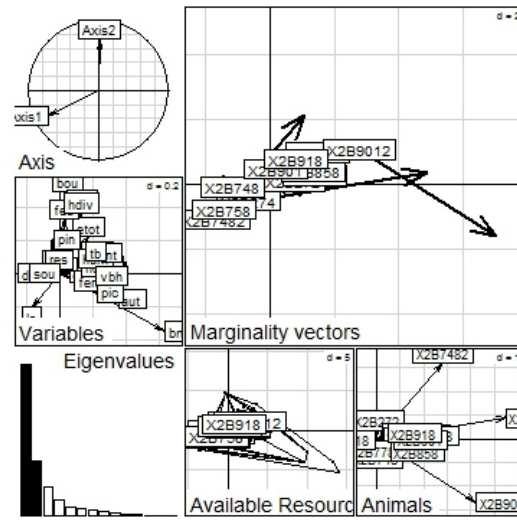


- Site du Plaix (Forêt de Tronçais) : *Myotis bechsteinii*.

a.

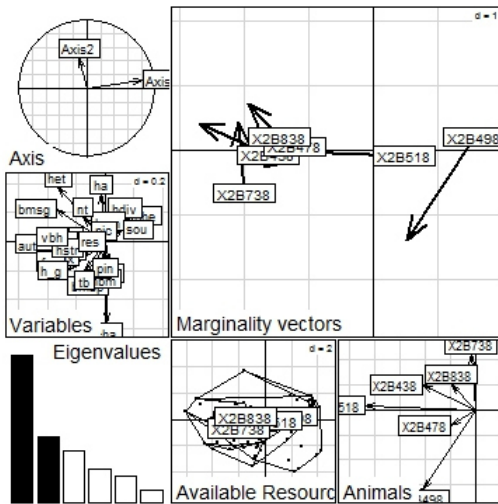


b.

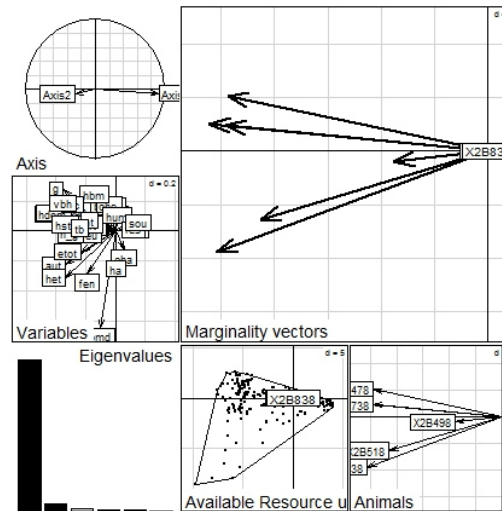


- Site de Saloup (Forêt de Tronçais) : *Myotis bechsteinii*.

a.

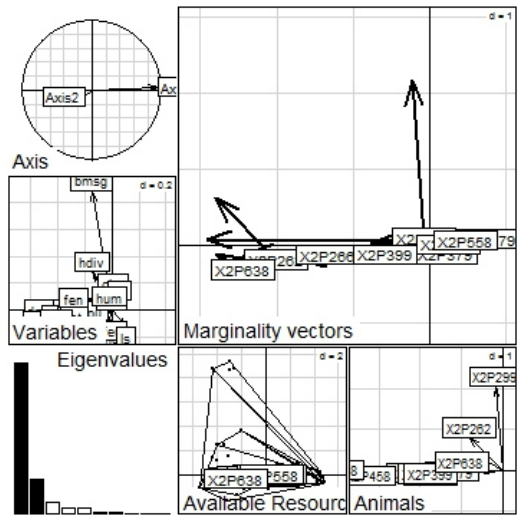


b.

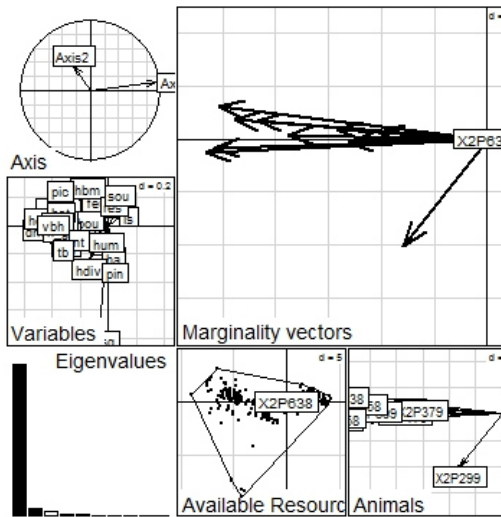


- Site de Saloup (Forêt de Tronçais) : *Plecotus auritus*.

a.

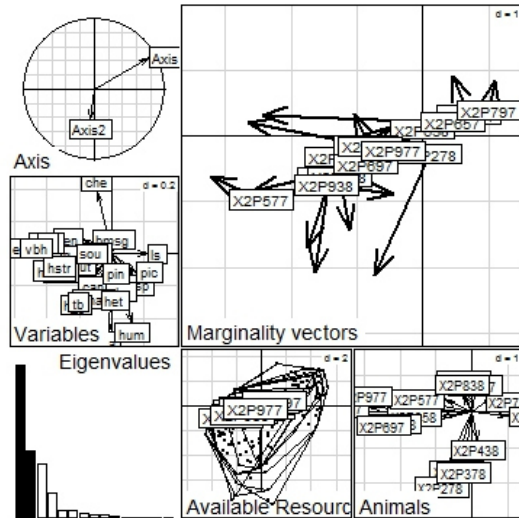


b.

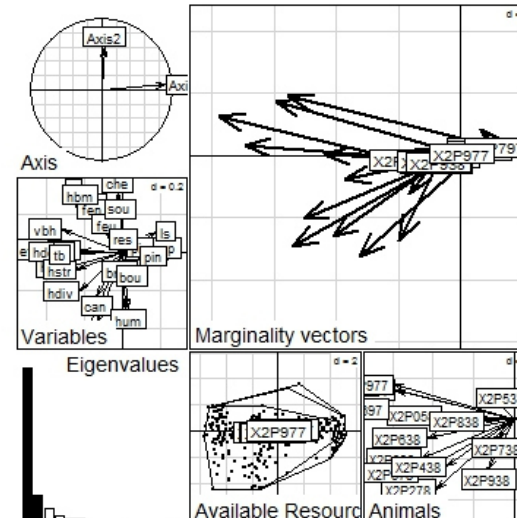


- Site de Vernigeole (Forêt de Tronçais) : *Plecotus auritus*.

a.



b.



## **Annexe 9 : Articles**

- How does deadwood structure temperate forest bat assemblages? (issu du chapitre 3)
- Tree Cavities used as Bat Roosts in a European Temperate Lowland Sub-Atlantic Forest (article préliminaire au chapitre 1)
- Tree selection by roosting bats in a European temperate lowland sub-Atlantic forest (article préliminaire au chapitre 1)

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# How does deadwood structure temperate forest bat assemblages?

Laurent Tillon<sup>1,2</sup> · Christophe Bouget<sup>3</sup> · Yoan Paillet<sup>3</sup> · Stéphane Aulagnier<sup>4</sup>

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**Abstract** Thirty percent of forest species depend on deadwood. Some of them are now considered rare or at high risk of extinction mainly due to an insufficient quantity of deadwood substrates. Some bats roost in dead trees and snags. Because European bats are strictly insectivorous, we can wonder whether deadwood plays an important role by providing potential preys too. We conducted ultrasonic surveys in different deciduous French forests dominated by oaks (*Quercus* spp.) and beech (*Fagus sylvatica*). Our results showed a positive relationship between the volume of deadwood and the richness of bat species. Some species were positively related to deadwood volumes, either lying or standing, with detected thresholds. Species richness increased particularly from 25 m<sup>3</sup> per hectare of standing deadwood. This link can be explained

by deadwood-dwelling preys or by changes in the forest structure, due to openings created by dead trees that are favorable for edge-habitat species. Other species negatively reacted to the presence of deadwood, either because bats were not able to forage there or because dead trees did not provide relevant preys. Contrary to our hypothesis, clutter by foliage and basal area of the living trees explained more the presence/occurrence of gleanings bats than deadwood. Whereas several species were considered as forest bats (*Myotis bechsteinii*, *Plecotus auritus*, *Barbastella barbastellus*), we did not find any relationship between their occurrence and deadwood. This result strengthens the need of further studies on the relationships between forest habitats and bat assemblages.

**Keywords** Chiroptera · Oak forest · Dead trees · Forest glade · Conservation · Forest management

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## Introduction

Standing and lying deadwood is a key element that preserves forest biodiversity (Jonsell et al. 1998; Bunnell et al. 2002; Müller et al. 2007; Müller and Bussler 2008). The response of organisms to the presence of deadwood in the forest varies widely: Fungi, lichens, bryophytes and saproxylic beetles are closely related to the local quantity and the diversity of deadwood (Franc et al. 2007; Müller and Bussler 2008; Lachat et al. 2012). Species richness is generally correlated with deadwood at the local level (Nilsson and Baranowski 1997; Grove 2002), even if it seems to depend on the local diversity of deadwood pieces rather than on their volume (Brin et al. 2009). Nevertheless, Bouget et al. (2013) showed that the local species richness of saproxylic beetles grew faster after the

threshold of 46 m<sup>3</sup> per hectare of lying deadwood. One might therefore expect a positive response of species that hunt these insects to the presence of deadwood, with the possibility to detect threshold effects of deadwood as their preys. However, studies show that the dead wood forest enrichment increases the richness of species that feed on saproxylic insects are largely lacking.

Deadwood can provide roosts for isolated or groups of bats and food resources. It is the case for some species in temperate North American forests dominated by conifers (Bunnell et al. 2002; Kalcounis-Rüppell et al. 2005; Barclay and Kurta 2007) and in Europe by *Nyctalus leisleri* and *N. lasiopterus* in cavities (Ruczynski and Bogdanowicz 2005; Beuneux et al. 2010), *Barbastella barbastellus* and some *Myotis* and *Pipistrellus* species regularly found behind peeling barks, particularly on snags (Russo et al. 2004; Pénicaut 2006; Hillen et al. 2010; Russo et al. 2010). Deadwood can also produce insects can be predated by bats, even if bats do not seem to be dependent on certain types of deadwood as standing deadwood (Zehetmair et al. 2015). Insects availability may be the main limiting factor for bats (Zahn et al. 2006). Dead trees represent also a significant source of potential preys, mainly beetles, but also some *Diptera*, *Dictyoptera*, *Hemiptera* and *Hymenoptera* whose larvae developed on deadwood. More than 30 % of all insect species in lowland temperate forests, and more than 40–50 % of forest beetles in some regions of the world, depend on deadwood (Good and Speight 1996; Dajoz 1998; Grove 2002). Some bat species are opportunistic while other ones are specialized for both diet and feeding habits, even if they are not restricted to one type of prey (see Table 1). Thus, the insects from the deadwood might be important prey for these species. Forest bats can benefit from outbreaks of beetles linked with fresh deadwood. For example, several bat species (especially genus *Pipistrellus*, *Eptesicus* and *Nyctalus*) have been reported to be hunting above barked harvested trees temporarily stocked in forests, which promotes a sudden concentration of bark beetles (Tillon 2001; Mehr et al. 2012). Thus, the opportunistic species (genus *Pipistrellus*, *Eptesicus* and *Nyctalus*) should be particularly dependent of deadwood volume for the production of their preys. The forest specialist species (gleaning bats, e.g., genus *Plecotus* and *Myotis*) should also benefit insects from the deadwood. In addition, bat species have different foraging strategies as well as different morphology and physiology that are often adapted to either dense or open foraging habitats (Jung et al. 2012; Müller et al. 2012). However, stratification of vegetation and foliage can also play an important role in the production of insects (Dajoz 1998; Burford et al. 1999; Ulyshen 2011), mainly *Diptera* (Gregor and Bauerova 1987) and *Lepidoptera* (Rydell and Lancaster 2000; Speakman and Rydell 2000; Jones and Rydell 2003) whose

most of larvae develop on leaves. Moreover, prey abundance increases with the mean vegetation density, and it seems that the bat activity depends more of forest habitat structure and vegetation than prey availability (Müller et al. 2012). So, bat activity in forests should be dependent on the density of vegetation and stand height, especially for gleaning species (Jung et al. 2012; Müller et al. 2012; Plank et al. 2012; Müller et al. 2013; Kennedy et al. 2014).

As bats activity seems more related to the structure of the habitat than prey availability (Müller et al. 2012), we expect a response from the activity of bats at different descriptive parameters of forest habitats. We hypothesized that the amount of standing and/or lying deadwood and/or the structure of vegetation explains local species richness of bats in temperate broadleaved forests as well as the level of foraging activity for most species and that thresholds of deadwood volumes can be detected. We therefore studied the feeding activity of bats in several French oak lowland forests where sampling plots were distributed according to the quantity of deadwood as a consequence of different forest management.

## Materials and methods

### Study areas

We sampled 132 plots of 20 m radius in six lowland forests present on the northern half of France, with a vocation of wood production but also maintaining biodiversity through forest reserves: 24 in Auberive–Chalmessin (Champagne), 25 plots in Chizé (Poitou), 10 in Citeaux (Burgundy), 29 in Fontainebleau and 30 in Rambouillet (Ile-de-France), and 14 in the Haut-Tuileau (Champagne) (Fig. 1). Of these plots, 73 were located in forest harvested for timber and 59 were located in forest reserves where management has been abandoned for at least 20 years (up to more than 150 years) (Fig. 2, Paillet et al. 2015). All these forests are dominated by oaks *Quercus petraea* and *Q. robur* accompanied by secondary species such as beech *Fagus sylvatica*, hornbeam *Carpinus betulus*, birch *Betula pubescens* and *B. pendula*, aspen *Populus tremula*, sorb tree *Sorbus torminalis* and wild cherry tree *Prunus avium*.

### Quantifying bat activity

Ultrasonic detection provides easy access to foraging bats in any type of environment. This is one of the methods most commonly used to inventory bats in forests (Boonman 1996; Kunz et al. 1996; Gannon and Sherwin 2004; Middleton et al. 2005; Lacki et al. 2007a, b; Barataud 2012). Ultrasonic detection has the advantage of detecting all species but in a limited range (5–40 m) depending on the

**Table 1** Functional group (foraging ecology and forest as foraging habitat) and diet (main prey) of bat species recorded in six French oak forest

Functional group	Species	<i>Rhinolophus hipposideros</i>	<i>Myotis bechsteinii</i>	<i>Myotis brandtii</i>	<i>Myotis daubentonii</i>	<i>Myotis emarginatus</i>	<i>Myotis myotis</i> *	<i>Myotis mystacinus</i>	<i>Myotis nattereri</i>
Foraging ecology	Closed-habitat forager	x	x	x	x	x	x	x	x
	Edge-habitat forager			x					
	Open-habitat forager								
Forest as foraging habitat	Yes		x	x	x		x	x	x
	Partly No	x			x	x		x	(x)
Diet	Specialized	x		x	x	x	x	x	x
	Opportunistic		x			X		x	+
Arachnida Diplopoda & Chilopoda Insecta	<b>Coleoptera</b>	x	X	x	+	+	X	+	+
	Dermoptera		X			+			
	<b>Dictyoptera</b>		X						
	Diptera	X	X	X	X	X	x	X	X
	Ephemeroptera			x	x	x		x	+
	<b>Hemiptera</b>		x	+				+	
	Homoptera		x						
	<b>Hymenoptera</b>	+	x					+	x
	Lepidoptera	X	X	x	+	+	+	x	x
	Neuroptera	X	X	x	x	+	+	+	+
	Orthoptera		X					x	+
	Plecoptera				+			+	+
	Psocoptera	x		+		+		+	+
	Trichoptera	x	x	+	x			+	x
	Species	<i>Nyctalus leisleri</i>	<i>Nyctalus noctula</i>	<i>Epptesicus serotinus</i>	<i>Pipistrellus pipistrellus</i>	<i>Pipistrellus pygmaeus</i>	<i>Pipistrellus kuhlii</i>	<i>Plecotus auritus</i>	<i>Plecotus austriacus</i>
Foraging ecology	Closed-habitat forager						x	x	(x)
	Edge-habitat forager		x	x	x	x			x
	Open-habitat forager	x	(x)						



Table 1 continued

Species	<i>Nyctalus leisleri</i>	<i>Nyctalus noctula</i>	<i>Eptesicus serotinus</i>	<i>Pipistrellus pipistrellus</i>	<i>Pipistrellus pygmaeus</i>	<i>Pipistrellus kuhlii</i>	<i>Plecotus auritus</i>	<i>Plecotus austriacus</i>	<i>Barbastella barbastellus</i>
Forest as foraging habitat	x						(x)		(x)
Yes									
Partly	(x)	x	x	x			x	x	x
No					x	x	(x)		
Specialized	x			x	x		x	x	x
Opportunistic		x	x						
Arachnida	+		+				+	+	
Diplopoda & Chilopoda						+			
Insecta									
<b>Coleoptera</b>	x	x	X	X		X			
Dermoptera							+	+	
<b>Dictyoptera</b>			+						
Diptera	X	X	X	X	X	X	+	+	+
Ephemeroptera	+	x		+		x			
<b>Hemiptera</b>		X	x	+		x			
Homoptera	+			X					
<b>Hymenoptera</b>	+	x	x	X					+
Lepidoptera	X	x	X	X	x	X	X	X	X
Neuroptera	x	+		X		x		+	+
Orthoptera		+	+						
Plecoptera		+		X					
Psocoptera				x					
Trichoptera	x	X	X	+	x	X	+	+	+

Functional group (foraging ecology and forest as foraging habitat) and diet (main prey) of bat species recorded in six French oak forest

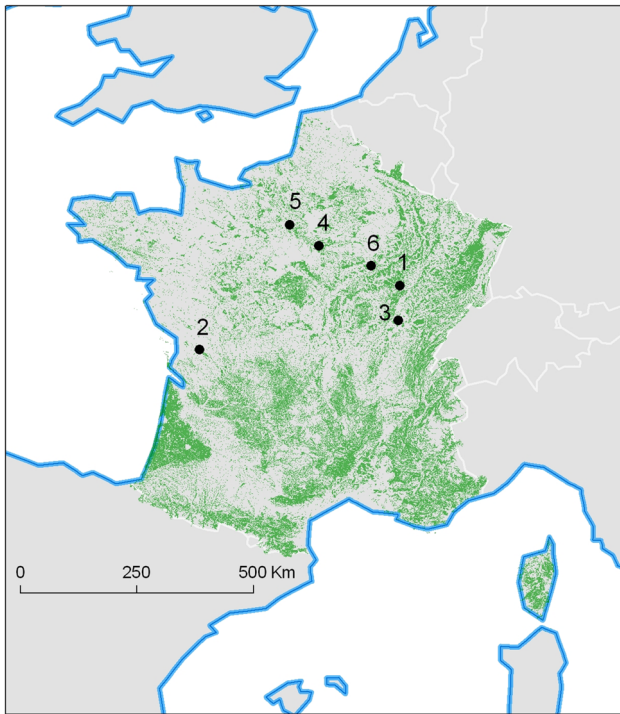
No studies on the diet of *Myotis alcatraz* have been conducted yet, due to its recent description. It therefore does not appear in this table

Functional group. x: for the main behavior and (x) for the accessory behavior of the species (Patterson et al. 2003; Barataud, 2012)

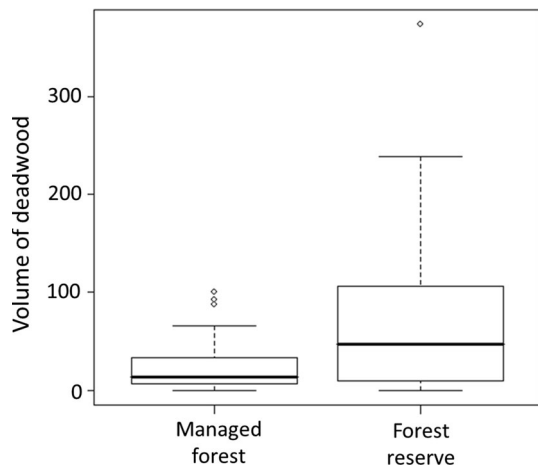
Diet. X: more than 20 % of occurrence in pellets, x: between 10 and 20 %, +: between 5 % (according to Beck 1995; Arlettaz 1996; Vaughan 1997; Roué and Barataud 1999; Arlettaz et al. 2000; Motte and Libois 2003; Bartonička et al. 2008; Kervyn et al. 2012; Lino et al. 2014)

Bold font designates orders of insects including taxa with larval saproxylic development

\* *Myotis myotis* is a gleaner species that hunts its prey above the ground mainly “by ear” (passive earings) (Arlettaz 1996), like *M. bechsteinii* in the foliage of trees (Siemers and Swift 2006)



**Fig. 1** Location of the six French oak forests sampled for the study of the relationship between bats and deadwood (1 Auberive–Chalmesin; 2 Chizé; 3 Citeaux; 4 Fontainebleau; 5 Rambouillet; 6 Haut-Tuiléau). The green areas represent the French forest cover. (Color figure online)



**Fig. 2** Total volume of deadwood (median and quartiles) per hectare ( $\text{m}^3$ ) in 73 plots of French oak forests harvested for timber and 59 plots in forest reserve without any management for at least 20 years or more 150 years

flying conditions and species. A site attractive for a given species is characterized by a locally high level of activity. The small size of plots of ultrasonic detection is so a major advantage for the use of ultrasonic detection and can link local descriptive variables of habitat to bat activity (Barataud 2012).

A pair of trained chiropterologists conducted point counts of 30 min at each plot, repeated three times, in April, June and September, between 2008 and 2011, provided that temperatures were always higher than  $5^\circ\text{C}$ , and that neither rain nor wind occurred, systematically during new moon (lunar illumination tends to adversely influence the emissions of bats, Barataud 2012). Point counts took place during the first 3 h after sunset. Each individual sequence of 5 s maximum was considered as a single contact. Two individuals heard at the same time were therefore counted as two contacts. Point counts were performed from the ground, thus excluding bat species emitting in short-range and foraging above the canopy (especially some *Myotis* and *Plecotus*, Plank et al. 2012; Müller et al. 2013; Tillon et al. in prep). This has been offset by the realization of the same point count in several passes. In April, gleanings bats must travel greater distances to find their prey, especially those that depend on the foliage of deciduous trees that have not yet ridden. In September, juveniles increase the number of individuals present in forests. In both cases, the probability of detection of the species is therefore increased (Tillon et al. in prep). We identified bats using additional methods of heterodyne and time expansion (Obrist et al. 2004; Barataud 2012). Each contact was determined to the species level whenever possible, or by default to genus for 8.32 % of contacts: 0 % for *Rhinolophus* group, 2.19 % for *Pipistrellus* and *Barbastellus* group, 14.83 % for *Eptesicus* and *Nyctalus* group and 45.52 % for *Myotis* and *Plecotus* group. We used Pettersson D980 or Pettersson D240 $\times$  bat detectors coupled with digital recorders Marantz PMD620. When a sound sequence was not identified by the heterodyne, we recorded it in time expansion (10 $\times$ ) for identification with BatSound 3.31 software and the identification keys of Barataud (2012). To integrate the difference between species detectability, Alpizar-Jara et al. (2004) suggest using an estimator of detection probability for each taxon. So the number of contacts was assorted with the species-specific detection probability proposed by Barataud (2012). Thus, *Rhinolophus hipposideros* and *Plecotus* sp. were assigned a coefficient of 5, *Myotis nattereri* and *M. emarginatus* a coefficient of 3.1, *M. alcahoie*, *M. brandtii*, *M. mystacinus*, *M. bechsteinii* and *M. daubentonii* a coefficient of 2.5, *Barbastella barbastellus* and *Myotis myotis* a coefficient of 1.7, *Pipistrellus pygmaeus* a coefficient of 1.2, *P. pipistrellus* and *P. kuhlii* a coefficient of 1, and for species with high signal range *Eptesicus serotinus* a coefficient of 0.83, *Nyctalus leisleri* 0.31 and *Nyctalus noctula* 0.25. The response of bats at different descriptive parameters of forest habitats can be expressed through the functional groups rather than the specific scale. Groups of species based on foraging ecology (Patterson et al. 2003; Müller et al. 2013; Table 1) were also investigated: *Myotis* and

*Plecotus* species = “closed-habitat foragers,” *Pipistrellus* and *Barbastella barbastellus* species = “edge-habitat foragers” and *Nyctalus* and *Eptesicus* species = “open-habitat foragers.”

### Description of forest habitats, measure of deadwood

Deadwood was measured according to procedures based on Paillet et al. (2015). For standing deadwood (SDW in  $\text{m}^3/\text{ha}$ ), all trees with a diameter at breast height (dbh) comprised between 7.5 and 30 cm were measured within a 10 m radius. Standing dead trees of more than 30 cm dbh were measured in a 20 m radius. We calculated the volume of recently dead and intact trees, using the single entry volume table of living trees. The volume of other deadwood (snags, high stumps...) was determined individually using dbh, height and a correction coefficient for diameter decrease. For lying deadwood, the volumes of pieces were measured using two methods. Dead trees having a diameter greater than or equal to 30 cm, and included in the plot of 20 m radius, were cubed by multiplying their length by their diameter (taking into account their decay). Dead trees having a diameter between 5 and 30 cm were counted and measured in three 20-m-long transects using the “line intercept sampling” (Marshall et al. 2000) in three directions from the center of the plot. Volume was then calculated using the measurements of each piece (intercepted diameter), the intercept angle of the transect and the probability of intercepting the piece of deadwood in plot (Marshall et al. 2000; Paillet et al. 2015). The sum of these two values gave the total volume of lying deadwood (LDW in  $\text{m}^3/\text{ha}$ ).

Whereas the vegetation and its clutter can influence the ability of detecting a species (Ford et al. 2005; Gonzalo-Turpin et al. 2008; Plank et al. 2012; Müller et al. 2013), we have included the cluttering vegetation as an explanatory variable of the activity. We measured the total basal area of live trees on each plot (BA.LW in  $\text{m}^2/\text{ha}$ ) to incorporate a live tree effect in order to oppose live trees to dead trees in the analyses. We visually classified the clutter of the vegetation into three classes (less than a third of the space around the observer occupied by vegetation in all directions, between one and two-thirds of the space, more than two-thirds of the space) within radius of 5, 5–25 and beyond 25 m, for horizontal and vertical vegetation. These values were summed to provide an index of total horizontal clutter (Htot) and an index of total vertical clutter (Vtot), ranging from 3 to 9. The two variables were normally distributed (Kolmogorov–Smirnov test,  $D = 0.053$ ,  $p = 0.851$ ). We tested the possible correlation between deadwood variables and clutter by vegetation variables with a Spearman correlation test.

The total volume of deadwood goes from 0 to  $122.45 \text{ m}^3/\text{ha}$  in managed forests as it goes from  $0.26$  to  $373.47 \text{ m}^3/\text{ha}$  in forest reserves (Fig. 2).

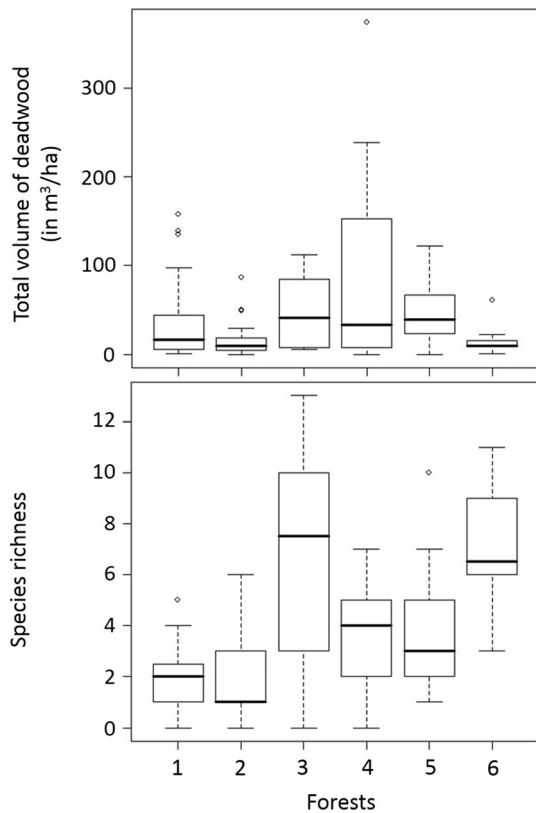
### Data analysis

Response variables of bat species assemblages (total species richness, total number of contacts (all species), occurrence and number of contacts of each species (or group of species) were related to predictors describing deadwood (SDW and LDW) and live trees (BA.LW, Htot and Vtot). We modeled response variables using generalized additive mixed models with Poisson error distributions for total species richness and number of contacts and with binomial error distributions for occurrence [R 3.0.2 software (R Development Core Team 2008), gam function of the *gam4* package]. Each model was generated with the set of five response variables. Since the species richness varied in the different forests, we added a random effect for forest in each model. Only significant variables ( $p < 0.05$  across all the models) were selected. Their contribution, i.e., their direction and magnitude across all the models, was indicated.

Breakpoint values were searched in species richness and species occurrence accumulation rates when significant relationships were revealed by the generalized linear models. Estimates of breakpoints were calculated with the full set of predictors by recursive partitioning by means of maximally selected two-sample statistics (Hothorn et al. 2006; Zeileis et al. 2008). Only primary and significant breakpoints ( $p < 0.001$ ) are reported. Based on 1000 bootstrap samples, 80 % confidence intervals (to define ranges more tightly than 95 % CI) were calculated for all breakpoints (*party* and *boot* R-packages). Contrary to other models used in this study, this method does not allow to take the clustered structure of the data (at least forest location) into account as a random effect.

### Results

The total volume of deadwood among plots ranged from 0 to  $373.47 \text{ m}^3$  per hectare (Fig. 3), with a mean  $\pm$  SD of  $43.65 \pm 58.61 \text{ m}^3$  per hectare of total deadwood ( $9.47 \pm 20.31 \text{ m}^3/\text{ha}$  for standing deadwood (SDW) and  $34.52 \pm 45.96 \text{ m}^3/\text{ha}$  for lying deadwood (LDW)). We did not find a correlation between the total clutter of vegetation and the volume of deadwood (Spearman correlation tests;  $p$  value = 0.46 for standing deadwood,  $p$  value = 0.15 for lying deadwood and  $p$  value = 0.20 for total deadwood). We recorded a maximum of thirteen bat species for one plot during a total time survey of 1.5 h, with an average of  $3.58 \pm 2.74$  species per plot (Fig. 3). Eighteen species



**Fig. 3** Total volume of deadwood in  $\text{m}^3/\text{ha}$  and bat species richness in 132 plots of six French oak forests (1 Auberive–Chalmessin; 2 Chizé; 3 Citeaux; 4 Fontainebleau; 5 Rambouillet; 6 Haut-Tuiléau). Boxplots represent medians and quartiles

were detected representing 5217 contacts (between brackets is the total number of contacts for each species) including *Rhinolophus hipposideros* (4), *Myotis alcaethoe* (10), *Myotis bechsteinii* (17), *Myotis brandtii* (9), *Myotis daubentonii* (58), *Myotis emarginatus* (63), *Myotis myotis* (20), *Myotis mystacinus* (34), *Myotis nattereri* (84), *Nyctalus leisleri* (291), *Nyctalus noctula* (202), *Eptesicus serotinus* (64), *Pipistrellus pipistrellus* (3823), *Pipistrellus pygmaeus* (44), *Pipistrellus kuhlii* (23), *Plecotus auritus* (1), *Plecotus austriacus* (2) and *Barbastella barbastellus* (34). Some sound sequences could not be identified to species, so the contact was assigned to a genus group: *Eptesicus–Nyctalus* group (97), *Myotis* group (222), *Plecotus* group (27) and *Pipistrellus* group (88).

### Total species richness and total number of contacts

Both standing deadwood and lying deadwood had a significant positive effect on species richness (Table 2; Fig. 4a–c). A threshold was detected only in the relationship between standing deadwood and species richness ( $T = 24.59 \text{ m}^3/\text{ha}$ , CI 80 % = [0.72–24.60]) (Fig. 5). Species richness decreased with the horizontal clutter of

vegetation (Fig. 4c), while the total number of contacts responded negatively to this variable (Table 2). The more the forest habitat was cluttered with horizontal vegetation (Htot), the less the bat species occurred. Nevertheless, a very active species, *Pipistrellus pipistrellus*, dominated the others by the number of contacts. We did not find any link between species richness and the total basal area of live trees (BA.LW) and vertical clutter (Vtot) (Table 2; Fig. 4d, f), and between the number of contacts and standing deadwood, lying deadwood, the total basal area of live trees and vertical clutter.

### Response of species group to deadwood volumes

Many occurrences for the group *Eptesicus* and *Nyctalus* influenced to a large extent the general results on the number of contacts. This phenomenon was explained by the great range of signals emitted by these species (up to more than 100 m in some situations). Conversely, the lack of occurrences for some poorly detectable taxa (only a few meters for *Plecotus* sp., *Myotis alcaethoe* and *Rhinolophus hipposideros*) did not allow us to perform the tests. All the results are presented in Table 2.

### Response of closed-habitat foragers

The occurrence of some closed-habitat forager species (*Myotis* and *Plecotus*) was positively explained by lying deadwood as the number of contacts. The number of contacts of this group was negatively influenced by the total basal area of live trees. The occurrences of *Myotis brandtii* and *M. emarginatus* showed a positively relationship, respectively, with the total basal area of live trees and horizontal clutter. The number of contacts of *M. emarginatus* showed a positive relationship with lying deadwood while the relationship was negative for *M. brandtii*. The total basal area of live trees favored the number of contacts of *M. myotis*. Horizontal clutter explained the number of contacts of *M. daubentonii*. *M. bechsteinii* and *M. nattereri* did not show any relation with deadwood, live wood and clutter of vegetation. No relationship was found between standing deadwood and vertical clutter and this group. No threshold in deadwood, live trees and vegetation clutter was observed in this functional group.

### Response of edge-habitat foragers

The occurrence and the number of contacts of edge-habitat forager species (*Pipistrellus* and *Barbastella barbastellus*) were positively associated with lying deadwood. A threshold was detected in this relation for the occurrence ( $T = 110.37$ , 80 % CI = [31.70–114.00], see Fig. 6e) and the number of

**Table 2** Results obtained from modeling species richness, total of contacts and the number of contacts per species with Poisson error distributions and occurrences of bat species in six French oak forests with a binomial error distribution

Taxon	Number of occurrences	SDW	LDW	B.A.L.W	Htot	Vtot	Number of contacts	Coefficient of detectability	SDW	LDW	B.A.L.W	Htot	Vtot
Species richness									0.005* (SE: 0.002)	0.002* (SE: 0.001)		-0.100* (SE: 0.048)	
Total of contacts												0.247* (SE: 0.111)	
<i>Rhinolophus hipposideros</i>	4	nc	nc	nc	nc	nc	2	5	nc	nc	nc	nc	nc
<i>Myotis alcathoe</i>	4	nc	nc	nc	nc	nc	10	2.5	nc	nc	nc	nc	nc
<i>Myotis bechsteinii</i>	11						17	2.5					
<i>Myotis brandtii</i>	7			0.226* (SE: 0.089)			9	2.5		-0.043** (SE: 0.016)			
<i>Myotis daubentonii</i>	19						58	2.5				0.440* (SE: 0.262)	
<i>Myotis emarginatus</i>	23						63	3.1		0.015* (SE: 0.006)			
<i>Myotis myotis</i>	9						20	1.7			0.213* (SE: 0.099)		
<i>Myotis mystacinus</i>	18				0.523* (SE: 0.242)		34	2.5					
<i>Myotis nattereri</i>	29						84	3.1					
<i>Nyctalus leisleri</i>	39						291	0.31		0.017*** (SE: 0.003)	-0.144*** (SE: 0.028)		0.599* (SE: 0.308)
<i>Nyctalus noctula</i>	20						202	0.25					
<i>Eptesicus serotinus</i>	18	0.051*** (SE: 0.014)		-0.089* (SE: 0.038)			64	0.83	0.022* (SE: 0.011)				
<i>Pipistrellus pipistrellus</i>	106						3823	1	0.014*				0.290*

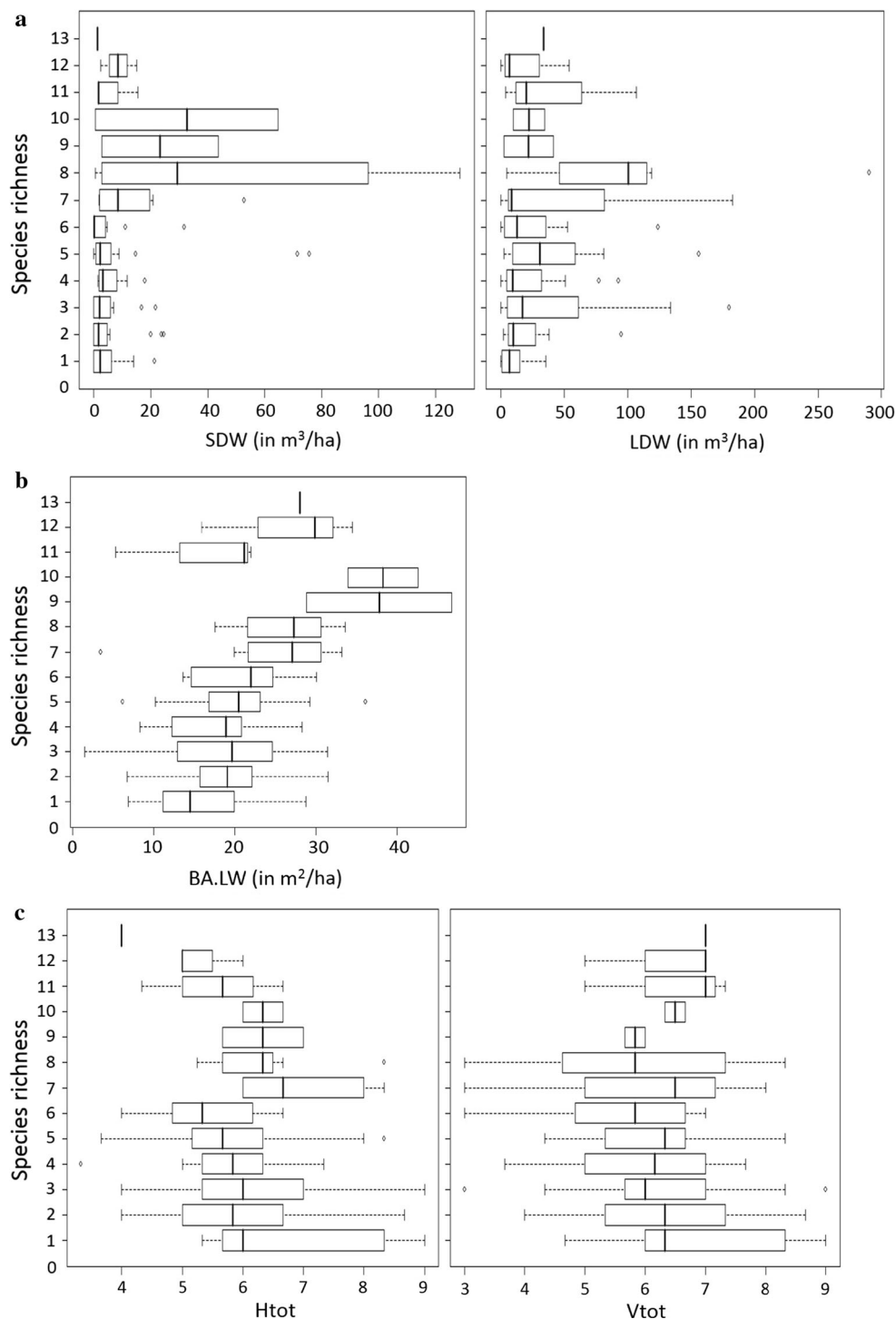
Table 2 continued

Taxon	Number of occurrences	SDW	LDW	B.A.LW	Htot	Vtot	Number of contacts	Coefficient of detectability	SDW	LDW	B.A.LW	Htot	Vtot
<i>Pipistrellus pygmaeus</i>	19			0.123**			44	1.2	(SE: 0.007)	0.008**		(SE: 0.141)	
<i>Pipistrellus kuhlii</i>	8			(SE: 0.043)	0.795* (SE: 0.417)		23	1		(SE: 0.003)			
<i>Plecotus auritus</i>	1	nc	nc	nc	nc	nc	1	5	nc	nc	nc	nc	nc
<i>Plecotus austriacus</i>	2	nc	nc	nc	nc	nc	2	5	nc	nc	nc	nc	nc
<i>Barbastella barbastellus</i>	15			0.089*			34	1.7			0.096*		
<i>Myotis and Plecotus</i>				(SE: 0.041)			547			0.016*** (SE: 0.004)	(SE: 0.041) -0.052* (SE: 0.025)		
<i>Pipistrellus and Barbastella</i>							4013			0.012***			
<i>Eptesicus and Nyctalus</i>		0.030*** (SE: 0.011)			0.857** (SE: 0.258)		654			0.026*** (SE: 0.009)			

Results are also presented after using coefficients of detectability to reflect the range of signals (Barataud 2012)

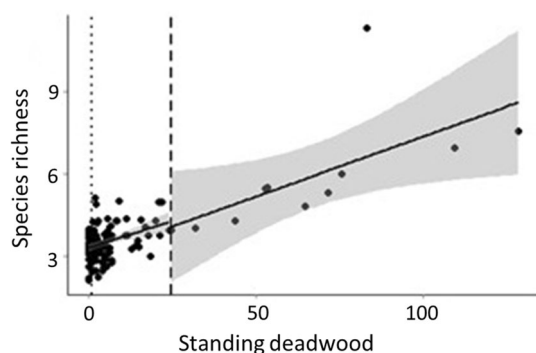
For each model, we noted the magnitude, with positive effect of the variable noted by (+) or negative by (-), the standard error (SE) and the significance of the variables, with critical thresholds: \*\*\* 0.1 %, \*\* 1 % and \* 5 %, for the volume of standing deadwood (SDW), the volume of lying deadwood (LDW), the basal area of live wood (B.A.LW), horizontal vegetation clutter (Htot) and vertical vegetation clutter (Vtot). Non-significant variables were not reported. Some models were not convergent or no interaction between the variables and the taxon was detected, corresponding in many cases to a problem of availability of data (the tests were not performed and the results are noted nc)

**Fig. 4** Species richness (SR) on sampled plots in six French oak forests related to **a** standing deadwood (SDW, m<sup>3</sup>/ha) and lying deadwood (LDW, m<sup>3</sup>/ha), **b** basal area of live wood (BA.LW, m<sup>2</sup>/ha), **c** horizontal vegetation clutter (Htot) and vertical vegetation clutter (Vtot)



contacts ( $T = 110.37$ , 80 % CI = [31.70–132.30], see Fig. 6b) for this group. *P. pygmaeus* and *B. barbastellus* met positively the total basal area of live trees for the occurrence. We found a threshold in the relation between the total basal area of live trees and the two last species, respectively, with  $T = 25.90$  m<sup>2</sup>/ha (80 % CI = [20.40–29.30]; see Fig. 6f) and  $T = 22.86$  m<sup>2</sup>/ha (80 % CI = [21.00–30.10]; see

Fig. 6c). The occurrence of *P. kuhlii* was positively related to horizontal clutter without detected threshold. For the number of contacts, *P. pygmaeus* was positively correlated with lying deadwood, while *P. pipistrellus* was positively correlated with standing deadwood. The number of contacts of *P. pipistrellus* was positively related to horizontal clutter. Finally, *B. barbastellus* met positively lying deadwood. We found a



**Fig. 5** Estimation of the breakpoint calculated by recursive partitioning (Hothorn et al. 2006) with respect to the relation between species richness and standing deadwood (in  $\text{m}^3/\text{ha}$ ) by means of maximally selected two-sample statistics ( $p = 0.002$ ). The breakpoint value is  $24.59 \text{ m}^3/\text{ha}$  (dashed line); the low 80 % CI is represented by the dotted line (the high confidence interval is the same that the breakpoint value)

threshold in the relation between the total basal area of live trees for the number of contacts of *B. barbastellus* only, with  $T = 29.49 \text{ m}^2/\text{ha}$  (80 % CI = [23.29–30.50]; see Fig. 6a). No relationship was found between vertical clutter and this functional group.

#### Response of the open-habitat forager group

The occurrence of open-habitat forager species (*Nyctalus* and *Eptesicus*) was positively influenced by an increase in standing deadwood and horizontal clutter and the number of contacts by an increase in standing deadwood only. Standing deadwood influenced positively the occurrence of *E. Serotinus*, with a significant critical threshold at  $T = 24.60 \text{ m}^3/\text{ha}$  (80 % CI = [14.70–24.60]; see Fig. 6d). Lying deadwood explained positively the number of contacts of *N. leisleri* while the relationship was negatively with the total basal area of live trees. The horizontal clutter was positively correlated with the number of contacts of *N. noctula*. Finally, *E. serotinus* was positively correlated with standing deadwood in the number of contacts and negatively related to the total basal area of live trees. No relationship was found between horizontal clutter or vertical clutter and this functional group.

## Discussion

### Deadwood as an explanatory variable for bats

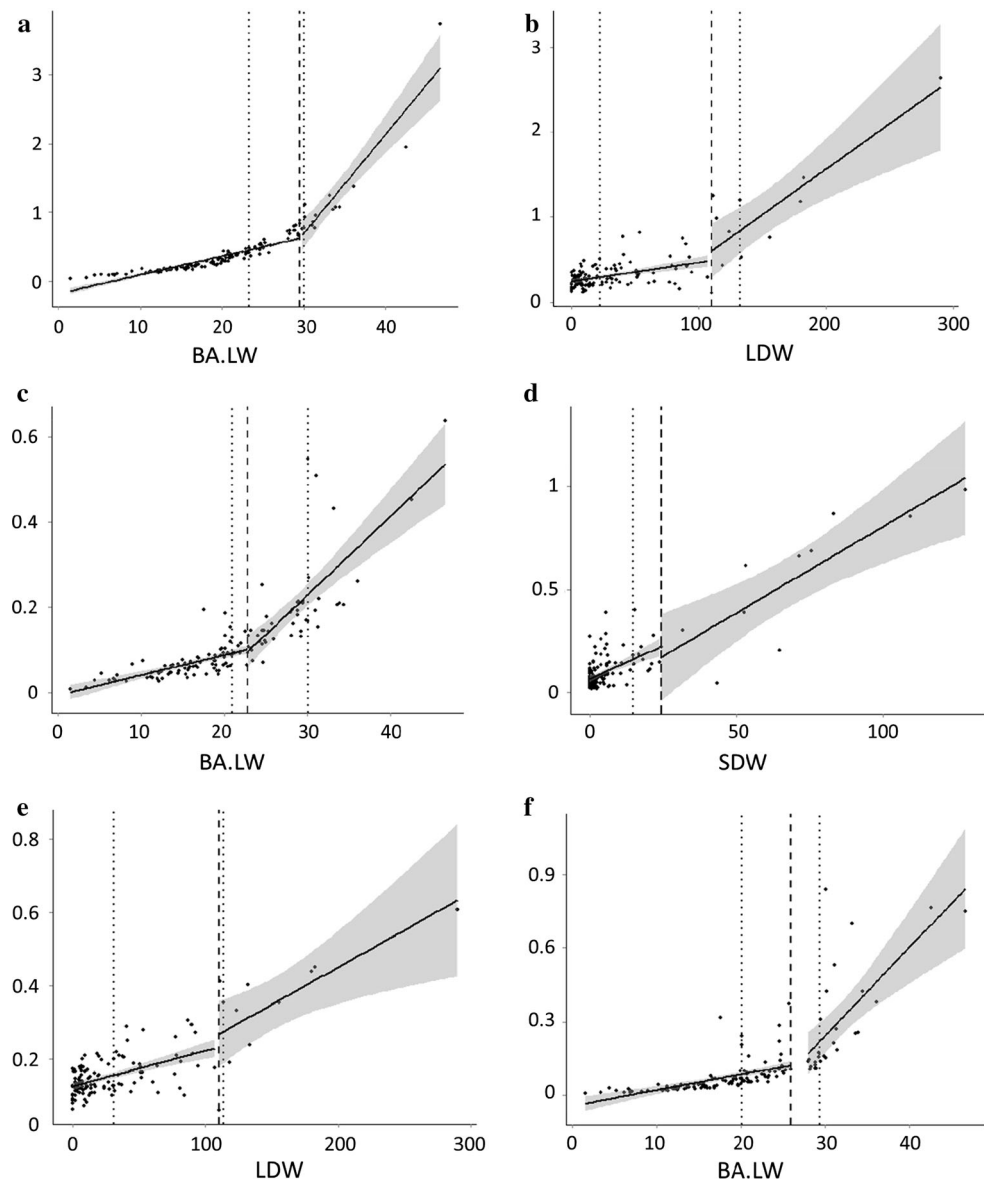
Our study showed that species richness responded positively to the volumes of standing and lying deadwood, as has been shown for other organisms (Franc et al. 2007; Müller and Bussler 2008; Paillet et al. 2010; Lachat et al.

2012), contradicting results of Zehetmair et al. (2015) who did not find a link between standing deadwood and bats. This species richness ranged from six to nine species in the deadwood richest plots/stands, even if we got up to thirteen species on some deadwood less rich stations (Citeaux forest). As for saproxylic beetles (Bouget et al. 2013), bat species richness increases more strongly from  $25 \text{ m}^3/\text{ha}$  for the standing deadwood, while it is more difficult to establish a link with lying deadwood. Our analysis of the number of contacts (all species) confirmed this trend. Bat species richness may increase up to a certain volume of lying deadwood; then, it would decrease because the ground habitats would not be available for some species, the habitat being too crowded to allow some species to move “freely” (i.e., *M. myotis* hunting in dead leaves on the ground).

Open-habitat foragers (*Nyctalus* and *Eptesicus*) respond positively to the volume of lying and standing deadwood. Indeed, these elements host insects that bats consume at emergence locations or in specific densities as *Eptesicus* sp. and *Nyctalus* sp. (Tillon 2001; Mehr et al. 2012). Effectively, saproxylic insects can provide an important part of available preys for predators as bats in forest (Dajoz 1998; Grove 2002). The presence of *E. serotinus* and *N. leisleri* influences predominantly the results obtained for this group of species. These species seek free spaces in their forested habitat to forage while maintaining benchmarks on which they can rely regularly with their sonar emissions. Their morphology and flight speed require a space completely clear of obstacles (Archaux et al. 2013; Müller et al. 2013). Forest clearings formed by deadwood (standing or on the ground) may therefore be favorable even if we did not detect a clear correlation between the increasing volume of deadwood and a reduction in clutter by vegetation. In addition, if a forest clearing forms naturally in the forest, it is probably after windthrow (this is the case in some stations located in reserves and with a lot of deadwood on the ground in the studied forests) or harvesting. The density of lying deadwood seems therefore favorable to the production of potential preys for *E. serotinus* and *N. leisleri*, either because it produces a habitat for insect larvae, or because the light reaching the ground contributes to the development of a diversified vegetation favorable to insects (Nilsson and Baranowski 1997; Dajoz 1998; Grove 2002). *E. serotinus* preys mainly on *Coleoptera* (some of them saproxylic) and large *Diptera* (especially *Tipulidae*) that grow in grassy and floral vegetations (Beck 1995). These vegetations are favored in the clearings. *N. leisleri* has a large diet range (with insects growing on deadwood such as some *Coleoptera*, *Diptera*, *Hymenoptera* and *Hemiptera*, or on ground vegetation such as certain *Diptera*, *Ephemeroptera*, *Lepidoptera* and *Neuroptera*) (Shiel et al. 1998; Dondini and Vergari 1999). This species can appreciate all



**Fig. 6** Estimation of breakpoints calculated by means of recursive partitioning by means of maximally selected two-sample statistics (Hothorn et al. 2006). Only primary and significant breakpoints ( $p < 0.001$ ) are reported. The breakpoint value ( $T$ ) is represented by the dashed line and the dotted lines represented the 80 % CI. A breakpoint was detected for the total number of contacts adjusted with the coefficient of detectability for *B. barbastellus* (a,  $T = 29.5 \text{ m}^2/\text{ha}$  for the total basal area of live trees) and for *Pipistrellus* sp. (b,  $T = 110.4 \text{ m}^3/\text{ha}$  for the lying deadwood) and for the occurrence of *B. barbastellus* (c,  $T = 22.9 \text{ m}^2/\text{ha}$  for the total basal area of live trees), *E. serotinus* (d,  $T = 24.6 \text{ m}^3/\text{ha}$  for the standing deadwood), *Pipistrellus* sp. (e,  $T = 110.4 \text{ m}^3/\text{ha}$  for the lying deadwood) and *P. pygmaeus* (f,  $T = 25.9 \text{ m}^2/\text{ha}$  for the total basal area of live trees)



available preys from these clearings with deadwood. Again, forest clearings with deadwood offer favorable internal forest edges that promote these species.

Among insects, *Diptera-Mycetophilidae* are numerous and varied in forest, and their production is independent of timber harvesting: they are strongly favored by fungi of standing deadwood (on which many larvae develop) and the abundance of high old trees (Økland 1996). However, these insects are present in 5–25 % of pellets of *P. pipistrellus* throughout the year (Arlettaz et al. 2000), confirming the hypothesis that the species particularly exploits clearings from standing deadwood in forests. A similar reasoning can be applied to *E. serotinus*, that is, in our study, favored by the standing deadwood and the associated saproxylic insects on which it feeds (Mehr et al. 2012).

Moreover, deadwood especially in large quantities may create an effect of clearing around a standing or lying dead trees. The volume originally occupied by the foliage of this tree then remains empty (only occupied by dead branches), allowing light to reach the ground. This ecological phenomenon has two effects: It helps to maintain a higher temperature in this glade in the first hours of the night, which is favorable for flying insects (Dajoz 1998; Müller et al. 2012) and it allows the development of undergrowth all around this clearing amplifying edge effects (Otto 1998). These edges are then used by bats to locate and forage. Deadwood may indirectly provide them with a favorable habitat structure. Indeed, we observed in our study that many bats (in *N. leisleri*, *E. serotinus* and *P. pipistrellus*) benefit greatly from the free volumes along the

edges created by the gap, as Müller et al. (2012), Archaux et al. (2013) and Müller et al. (2013) have observed previously.

Finally, *M. emarginatus* is the only one among closed-habitat foragers to reveal a link with the deadwood, when it is on the ground. The study of its diet shows that this species especially feeds on *Arachnida*, *Diptera*, *Coleoptera*, *Hemiptera* and *Hymenoptera*, some larvae of which develop on deadwood. In addition, the species primarily feed on spiders, which are often present on herbaceous vegetation or between tree branches to the ground (personal observations). Thus, individuals of the species chasing the prey are easily detectable by an observer on the ground.

### Species not sensitive to the presence of deadwood and influence of live trees

Deadwood volumes influenced less than half of the bat species studied. Meschede and Heller (2003), Barataud et al. (2009) and Zehetmair et al. (2015) suggest a likely strong link between the European forest bats and natural unmanaged forests with high deadwood volumes. Then, closed-habitat foragers (*Myotis* and *Plecotus*) show a positive relationship with lying deadwood. However, no species of this group except *M. emarginatus* showed a positive relationship with this compartment. Most forest bats of the genus *Myotis* and *Plecotus* and *Rhinolophus hipposideros* did not respond to the presence of deadwood and even showed a negative relationship (as *M. brandtii* with lying deadwood). Except for *P. pipistrellus* and *E. serotinus*, our analyses showed no relationship between the standing deadwood. However, some species are known to use these trees to roost in colonies, in particular *M. mystacinus*, *M. brandtii*, *M. alcahoie* and *B. barbastellus* (Meschede and Heller 2003; Russo et al. 2004; Pénicaud 2006; Hillen et al. 2010). Weak occurrences of the species in this group may partly explain this result. However, as lying deadwood is unevenly distributed in forests (this is especially the case in the French lowland deciduous forest (Vallauri 2005)), insects that depend on them are in the same way dispersed in the forest landscape (Bouget and Gosselin 2012). If bats of this group exploit these preys, it is only marginally and opportunism, as shown in their diet. No species of this group is specialized on these preys. Thus, our results are probably closer to reality despite the low statistical power of specific analyses.

The fact that there is no relationship between the deadwood and most considered forest species as *M. bechsteinii*, *M. nattereri*, *P. auritus* and *P. austriacus* (discrete species that benefits from the weighting of contacts through the use of coefficients of detectability) is difficult to explain. Considering the diet of these species, we rather

understand the positive relationship with the clutter of vegetation than a negative effect of deadwood. Our results for *Myotis bechsteinii*, a very territorial species (Kerth and König 1999; Barataud et al. 2009), reinforce this hypothesis. Indeed, this species would benefit from insects found on its home range, without focusing on saproxylic insects. In general, *Diptera* and *Lepidoptera* (depending on foliage) dominate in the forest (Dajoz 1998) and in the diet of these species. They make up a significant part of their diet with other insects dependent on vegetation such as *Dermaptera* and *Neuroptera* (Taake 1993; Wolz 1993; Dondini and Vergari 1999). *M. bechsteinii* also eat *Coleoptera*, whose larvae can develop in some deadwood. But some of these insects can be mobile and disperse in the forest canopy, in the undergrowth and in the forest edge (Bouget and Gosselin 2012). So *M. bechsteinii* is not especially dependent on prey from deadwood. However, when deadwood exists, the species can probably benefit from it in an opportunistic way. The dispersal abilities of insects and bats may explain the difficulty in showing a relationship between deadwood and bats. We can argue a similar hypothesis of a relationship to deadwood (and associated insects) for the other gleaning bats.

However, various studies have shown that density and stratification of vegetation could explain the selection of forest habitats for several species (Meschede and Heller 2003; Müller et al. 2012, 2013), or that species richness was highest in the foliage of trees, especially in canopy (Lacki et al. 2007a, b; Kennedy et al. 2014). Our results indicated first that the species richness of bats in forests depends more on deadwood (standing and lying) than on vegetation density (only horizontal clutter of vegetation). In addition, when the clutter becomes too dense, the richness decreases. A North American study showed that in bat species, richness increased with the clutter of vegetation but declined after a cluttering threshold (Hayes and Loeb 2007). Dense vegetation could limit access to the site for the fast flying species. Edge-habitat foragers (*Pipistrellus* and *Barbastella*) and open-habitat foragers (*Nyctalus* and *Eptesicus*) could not forage in those spaces, even if prey species abundance is high, in agreement with the results of a study conducted in German forests on the same species (Rieger and Nagel 2007). Closed-habitat foragers (*Myotis* and *Plecotus*) do not have this problem and can evolve in foliage (Patterson et al. 2003; Ford et al. 2005; Guldin et al. 2007; Jung et al. 2012; Plank et al. 2012; Müller et al. 2013). For these gleaning species, our results also show a generally positive relationship with the horizontal clutter of the live trees (for *M. brandtii*, *M. daubentonii*, *M. myotis* and *M. mystacinus*), reinforcing the hypothesis that foliage plays the leading role for the gleaning closed-habitat foragers and vegetation prevails over deadwood to explain the selection of a foraging habitat for the gleaning bats as

suggested by Mehr et al. (2012). Sometimes indeed in some populations of *M. nattereri*, individuals eat bark beetles (Swift 1997). However, these insects develop mainly on dying trees or trees dead for less than a year (Dajoz 1998). The relationship between this insect and the deadwood is therefore weak. In addition, *M. nattereri* as *P. auritus* seems to have a relatively specialized diet on foliage arthropods (Gregor and Bauerova 1987; Shiel et al. 1991; Swift 1997) and appears not to be very territorial (Tillon et al. in prep.). Individuals of these species must cover as much volume of foliage as necessary to find food without focusing on a specific site on a daily basis. In fact, because a volume occupied by lying deadwood on the ground is correlated with less foliage density, so no potential prey, our result probably reflects avoidance behavior of these sites with deadwood to favor stations of denser vegetation strata (or dense canopy, inaccessible to our surveys), joining the assumption of Jung et al. (2012), Mehr et al. (2012), Müller et al. (2012) and Plank et al. (2012) who showed an enhanced level of activity for gleaning species on densest vegetation strata in forest.

Finally, the increase in basal area of live trees thus indirectly promotes *M. myotis* and *B. barbastellus*. *M. myotis* mainly eats ground beetles (insects that do not strongly depend on deadwood) and forages at low elevation, requiring relatively clear undergrowth, at least in some spots (Arlettaz 1996). However, when basal area of live trees increases, less light reaches the ground because it is intercepted by the foliage, limiting the development of herbaceous and shrub vegetation (Otto 1998). *M. myotis* can thus forage on the ground. *B. barbastellus* is also favored by the increase in basal area of live trees. This species eats primarily *Lepidoptera* (Rydell et al. 1996; Sierro and Arlettaz 1997), most species of which do not depend on deadwood (Thorn et al. 2015). The increase in live trees is associated with the amount of foliage (in canopy and undergrowth), so the potential amount of *Lepidoptera* would increase (Dajoz 1998; Otto 1998). We therefore confirm the results of Russo et al. (2010) who highlighted the lack of relationship between this species and deadwood.

### Methodological limits

We encountered difficulties in detecting certain species during our study, especially closed-habitat forager species (*Myotis* and *Plecotus*). This phenomenon is widely known and requires to analyze results of studies based on ultrasonic detection with caution (Rieger and Nagel 2007; Weller 2007; Barataud 2012; Mehr et al. 2012). For example, Tillon et al. (in prep.) showed that *M. bechsteinii*

is very difficult to detect from the ground, especially when foliage (undergrowth) is dense and multistratified. Plank et al. (2012) even consider that this species is a specialist of foraging in canopy, like other species (*M. alcaethoe* particular). Moreover, *M. bechsteinii* can forage in passive listening, without ultrasound emissions (Siemers and Swift 2006). It is therefore likely that the presence of *M. bechsteinii* and *M. alcaethoe* is strongly underestimated in our inventories, especially on dense vegetation stations.

### Management recommendations

We showed that a volume of 25 m<sup>3</sup>/ha of standing deadwood seems sufficient to maximize species richness of bats while promoting species that depend on deadwood. It is more difficult to foster a value of lying deadwood because the threshold that we obtained in our study was of 110 m<sup>3</sup>/ha, only for *Pipistrellus* sp. In plots harvested for timber, this value is very high and can be difficult to implement for the manager. But if one is only interested in standing deadwood, in one hectare of forest with trees of 35 m high and a decay coefficient of 0.8 with a 15 m height of trunks usable for industrial wood, the manager needs to maintain 9.3 trees of 35 cm diameter (dbh), 4.5 trees of 50 cm (dbh) or 2.3 trees of 70 cm (dbh) to reach the volume of 25 m<sup>3</sup>/ha. This proposal is realistic. Imagining that all the trunks are removed by logging, it is also possible to maintain the crowns in cuts, not dismembering them, contributing to the maintenance of deadwood on the ground. We therefore propose to tend toward these values in managed forests, keeping as many standing deadwood (which can also be used to roost) as deadwood on the ground. In both cases, this should encourage the production of potential prey (from deadwood or ground vegetation favored by the increase in light) and the creation of favorable structures for the species that forage on edge (open-habitat and edge-habitat foragers). Managers may benefit from storms to maintain forest patches without harvesting. This would constitute an essential step to participate in the conservation of these species in forests. Finally, if these measures are designed to promote species richness and deadwood-dependent species, forest management must also consider the need to maximize the stratification of vegetation for the benefit of gleaning species.

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## Tree cavities used as bat roosts in a European temperate lowland sub-Atlantic forest

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The availability of suitable roosts may be the major limiting factor for maternity colonies of bats in forests. Most studies on the use of tree cavities by bats have focused on analysing occupancy by a single species, and not by the entire bat community. To provide guidelines for forest management conducive to sustaining bats in a temperate lowland European forest, we studied the occupancy of tree cavities by bats of all species. In six different habitat types of 4 to 10 ha, all tree cavities were recorded and described according to 47 qualitative and quantitative descriptive variables. Logistic regression analyses were computed to predict the occupancy of cavities by bats, and to identify the most relevant variables for use as bat roosts. With or without potential competitors in the analyses, bats mainly used cavities in healthy main branches, with a large entrance located high above the ground. They did not use peeling bark or cavities on secondary branches, nor cavities covered by spider webs. Despite a large number of potential roosts in the area, bats tend to be selective and the types of roosts were less diverse than described in the literature. Not surprisingly guidelines for forest management aimed at bat conservation include keeping healthy old trees, which provide various types of cavities.

*Key words:* bats, community, tree roost, temperature, forest management

### INTRODUCTION

The distribution of bats in areas with temperate climates is likely determined by several factors including: altitude, water availability, urban development, and forest or tree cover (Jaberg and Guisan, 2001). Forest habitats are used both for foraging and roosting (e.g., Kalcounis-Rüppell *et al.*, 2005; Lacki *et al.*, 2007). As bats are able to forage in various habitats, tree cavities are considered to be the most limiting factor for bats in forests. This is especially true for maternity colonies, which have more specific requirements, including a set of cavities available within a small area (Kunz and Lumsden, 2003; Meschede and Heller, 2003). For all bats, tree cavities must provide protection against adverse weather conditions such as wind, rain and extreme temperatures and against predators (Kunz and Lumsden, 2003; Barclay and Kurta, 2007). They also play a role in social interactions among individuals (Kerth *et al.*, 2001b; Willis and Brigham, 2004).

Most studies on forest bat roosts focus on a single species and aim to assess preferences, mainly

during the maternity period (Swift, 1997; Betts, 1998; Hurst and Lacki, 1999; Boonman, 2000; Menzel *et al.*, 2002; Ruczyński and Bogdanowicz, 2005). Some authors consider temperature as a critical variable driving the selection of tree cavities by bats (Kerth *et al.*, 2001a; Sedgely, 2001). In some cases, thermal environment inside the cavity appears to be an important factor in its selection by bats (Entwistle *et al.*, 1997; Kalcounis and Brigham, 1998).

Some species are relatively selective of specific roost types. For example, *Myotis brandtii* and *Nyctalus leisleri* prefer cavities resulting from natural degradation (Sachanowicz and Ruczyński, 2001; Ruczyński and Bogdanowicz, 2005, 2008). Other species choose roomy cavities (Willis *et al.*, 2006). Most species select cavities with small openings that limit access to predators (Ruczyński and Bogdanowicz, 2005) or competitors (Bonar, 2000; Blondel, 2005; Tillon, 2005).

Studies underline the preference of maternity colonies for cavities such as gaps under peeling bark, narrow cracks, large cracks opening upwards

or woodpeckers' hollows high above the ground with a small entrance (Pénicaud, 2002; Meschede and Heller, 2003). These types of natural cavities are related to the species of the tree and its age (Meschede and Heller, 2003).

Given that studies dealing with communities of temperate forest-dwelling bats mostly originate from North American coniferous forests (Kalcounis-Rüppell *et al.*, 2005; Brigham, 2007), with a few from Central Europe (Boonman, 2000; Ruczyński, 2004) where the climate is continental or rainier, and species richness of bats lower than in sub-Atlantic forests (12 to 13 species against more than 20 species on average in the forests of this region). We assessed cavity availability in a large lowland sub-Atlantic forest to provide guidelines for sustainable forest management aimed at bat conservation. Given the size of the area, we restricted our survey to several plots representative of different types of management. Our main objective was to predict the use or non-use of cavities by maternity colonies of all species known in the study area (main target for conservation purpose), to minimise the impact of future timber harvesting.

We recorded and described all potential bat roosts according to a set of variables gathered in broad categories: type of cavity, position on the tree, health condition of the tree next to the cavity, inner and outer dimensions, description of entrance openings, potential competitors and temperature (inside and outside cavities). Then we analysed the roost selection by modelling use (direct observation, guano, urine) and non-use of tree cavities.

## MATERIALS AND METHODS

### Study Area

The 22,000 ha Rambouillet forest is 70 km south-west of Paris, in the Paris Basin. This deciduous forest is dominated by *Quercus petraea* and *Q. robur* in its upper stratum, with secondary tree species such as *Betula* sp., *Populus tremula*, *Fagus sylvatica*, *Carpinus betulus*, *Prunus avium*, *Sorbus torminalis*, *Fraxinus excelsior* and *Castanea sativa*. Conifers cover almost 20% of the area.

The study was restricted to six deciduous stands dominated either by oak trees or by a mixture of oak and beech trees in the upper stratum. The selected plots varied from 4.5 to 10 ha, to include a quite large number of cavities per plot (minimum 30).

The forest is inhabited by 19 species of bats, including *Myotis bechsteinii*, *Plecotus auritus*, *Barbastella barbastellus*, *Myotis nattereri*, *Nyctalus noctula*, *N. leisleri*, *Myotis mystacinus*, *M. daubentonii*, *M. alcaethoe*, *Eptesicus serotinus*, *Pipistrellus kuhlii*, *P. pipistrellus*, *P. pygmaeus*, *P. nathusii*, *Rhinolophus hipposideros* and *Plecotus austriacus* (Tillon, 2007).

### Cavity Search

Within each plot, every cavities likely suitable for *Pipistrellus pipistrellus* (a space 1 cm wide is enough) were described. Even when climbing trees to reach cavities (O'Donnell and Sedgely, 1999), direct observation of bats in cavities is unlikely since tree-dwelling bats often shift roosts. Signs of bat use (guano, urine) were thus used as evidence of occupancy, at least in the case of maternity colonies (Willis *et al.*, 2006). We looked into each cavity less than 5 m high from a ladder, and climbed the trees to reach the higher cavities. We examined 565 cavities between April and October 2003.

### Description of Cavities

Each cavity was investigated using a set of (dentist) mirrors and a medical endoscope (4.5 mm in diameter and 60 cm in length). Traces of use and observations of animals (including potential competitors) were recorded; all bat species being pooled for data analysis. Cavities were measured with a graduated flexible wire, both above and below the entrance (inner diameter, inner height above the entrance, depth below the entrance, total vertical dimension, outer diameter of the tree at the cavity). Additional recorded variables included cavity origin, type and estimated age, as well as the condition of the surrounding wood and the orientation of the entrance.

Whichever the number of entrances for one cavity, each entrance was described, including its position on the tree and for the cavity, its diameter, length and orientation, any obstacle (nature and proportion of obstruction) at or in front of the opening (nature and distance), and the presence and position of poly-pores (lignicolous mushrooms).

### Presence of Potential Competitors

Any sign of use of the cavity by other animals was also recorded to take into account potential competition. We found no evidence of other mammals. All evidence of birds was pooled by species. Insects were classified into social species (Hymenoptera such as *Vespa crabro*) or species associated with wood decay. Spider webs were also recorded.

### Data Analysis

To predict the use or non-use of cavities by bats (dependant variable), we computed logistic stepwise regressions using the SPSS software (version 9.0, Norusis, 1999). This method is the most appropriate for analysing the presence or absence of a character when there are numerous qualitative and/or quantitative variables (whatever their distribution) (Keating and Cherry, 2004). We used the 12 quantitative variables recorded in the field. For qualitative variables, each category was considered as a variable noted either present (1) or absent (0), except when the different categories represented successive states. The set of variables (47) is listed in Table 1.

The number of cavities used by bats was much smaller (52) than the number of unused cavities (513), thus too small to obtain balanced predictions. The proportion of 1/3 of bat-used cavities to 2/3 of unused cavities proved to be the most appropriate. To use the variability of the whole set of data, we computed 10 analyses with 10 different re-samplings of 104 unused cavities. We then calculated the mean percentage of correct predictions



TABLE 1. Variables recorded on each tree cavity in the six sampled sites in the Rambouillet forest (France) to predict their use or non-use by bats

Variable	Description
Cavity size (in cm)	Outer and inner diameter (of trunk or branch) at the level of the entrance Depth and height below the entrance
Type of cavity (9)	Gap under bark, horizontal tube, vertical downward tube, vertical upward tube, vertical upward and downward tube, column with several openings, crack, peeling bark with wood degradation, various recesses
Condition of wood	Six classes from healthy to completely decayed
Origin of the cavity (7)	Lightning, large, medium or small woodpecker hollow, age-related decline of the tree, frost crack, detaching bark
Position of the cavity on tree	Support (3): trunk, main branch, secondary branch Orientation (8): north, north-east, east, south-east, south, south-west, west, north-west
Entrance characteristics	Total number of openings Height of each opening above the ground (in m) Width, height and length of openings (in cm) Obstruction of each opening (in cm) Cause of obstruction (2): natural or animal-made Position on tree (3): trunk, main branch, secondary branch Presence of obstacle in flight path (yes / no), distance to the first obstacle in flight path (in m) Presence (yes/no) and number of polypores near the entrance

and, for each variable, the mean regression coefficient  $\beta$  (the regression coefficient gives a relative contribution of the variable in relation to the prediction, positive values denoting that the variable contributes positively to the-use of cavities by bats) and the mean Wald statistic (which tests the statistical significance of the regression coefficient and thus the contribution of each variable; this statistic follows a  $\chi^2$  distribution for large samples).

Two sets of 10 logistic regressions were computed. The first set, using only the descriptive variables, aimed to explain the use of cavities regardless of the presence of other animals there. The second set was supplemented by the presence or absence of potential competitors or spider webs. At last, the occupancy of cavities was analysed for variables identified by each set of 10 models using Student's t tests (or Mann-Whitney tests in case of large variances) and  $\chi^2$  tests. The level of significance was 0.05 corrected for multiple comparisons.

### Temperature

On each study site, we fitted temperature data loggers (Hobo Tidbit; 32,000 events, precision 0.01°C) inside (just below the entrance) and outside cavities, between the end of April and the beginning of September (data recorded every five minutes). Over a total of 30 monitored cavities, 10 were used by maternity colonies. The equipped cavities were the most diverse in terms of shape, origin and orientation. None were used by bats over the whole logging period due to roost switching of colonies.

Inside and outside temperatures per 10-day periods (mean, maximum and minimum) were analysed using general linear models (function lme of R software — R Development Core Team, 2008). We tested several factors: location of the cavity (site, orientation, height above the ground), as well as the use versus non-use by bats.

## RESULTS

### *Diversity of Cavities*

Most available cavities ( $n = 513$ ) were cracks, gaps under bark and medium woodpecker hollows (Fig. 1A). Evidence of wood decay (peeling bark with wood degradation, base of dead branch, various recesses linked to natural decay of the wood, rotten wood, rotten core) was recorded in 35% of cavities (Fig. 1B). Used cavities ( $n = 52$ ) were mostly cracks and woodpecker hollows (75%), the remainder being various recesses linked to wood degradation (Fig. 1B). This preference for cracks and woodpecker hollows was statistically significant ( $\chi^2 = 28.01$ ,  $d.f. = 7$ ,  $P < 0.001$ ). The bat colonies found in other types of cavities (mainly under peeling bark) were mostly of pipistrelle species.

### *Main Features of Cavities*

Logistic regressions predicted the use ( $91.1\% \pm 2.4\%$ ) versus non-use ( $75.4\% \pm 7.7\%$ ) of cavities better, despite efforts to balance predictions. Six variables explained the selection of tree cavities by bats best in more than half the models (Table 2). These variables were the height of the opening ( $n = 10$  models), the condition of the wood around the cavity ( $n = 9$ ; the negative value of  $\beta$  indicates that selected cavities were mostly in healthy wood),

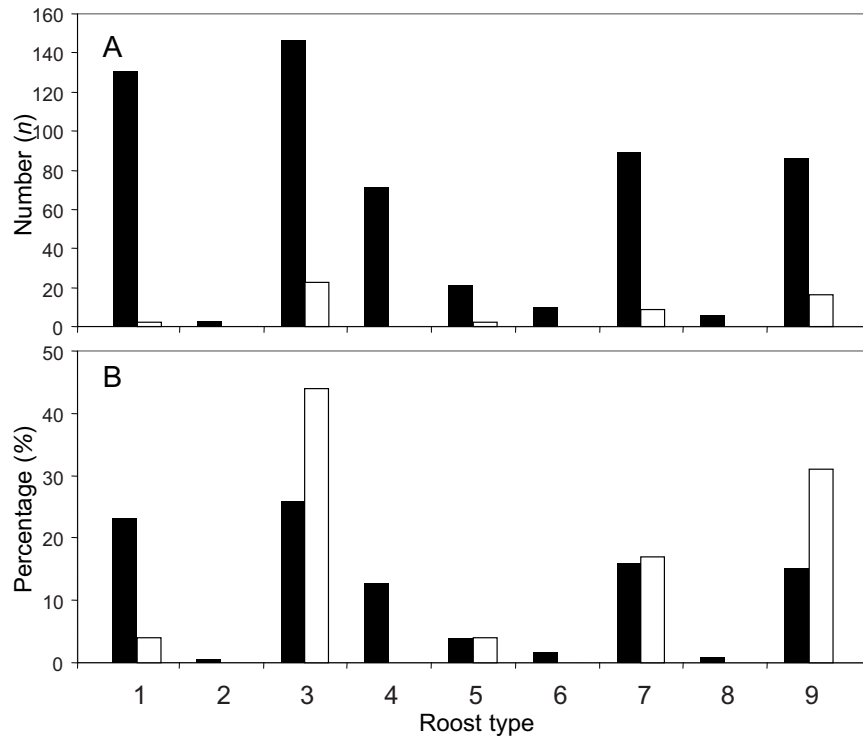


FIG. 1. Main cavities available (black bars,  $n = 565$ ) and used as bat roosts (white bars,  $n = 52$ ), expressed in terms of their number (A) and frequency (B), in trees of the Rambouillet forest (France). Roost type: 1 — Bark: gap under bark, 2 — Bark: peeling bark with wood degradation, 3 — Wood: crack, 4 — Wood: base of dead branch, 5 — Wood: recess linked to natural decay of the wood, 6 — Wood: rotten surface, 7 — Wood: rotten core, 8 — Hollow: large woodpecker, 9 — Hollow: medium woodpecker

the ‘peeling bark’ type of cavity ( $n = 9$ ), the height of the opening above the ground ( $n = 7$ ), the position of the cavity on a secondary branch and its inner depth below the entrance ( $n = 6$ ). The height of the opening was slightly greater in used than in unused cavities ( $74 \pm 254$  cm versus  $54 \pm 108$  cm respectively), the difference being nearly significant (Mann-Whitney,  $W = 14930.5$ ,  $P = 0.065$ ). Cavities used by bats tended to be located higher above the ground than other cavities ( $8.75 \pm 3.08$  m vs.  $7.01 \pm 4.08$  m;  $t = 2.99$ ,  $d.f. = 568$ ,  $P < 0.01$ ), and also to have a greater inner depth below the entrance ( $11.8 \pm 17.6$  cm vs.  $4.4 \pm 13.1$  cm;  $t = 3.75$ ,  $d.f. = 546$ ,  $P < 0.001$ ). Roosts were significantly more often located in the healthy part of the tree than in dying, dead or decaying parts ( $\chi^2 = 24.08$ ,  $d.f. = 2$ ,  $P < 0.001$ ).

Considering the different types of cavities: (i) gaps under peeling bark (only two were used out of 152 available) and horizontal tubes tended to be avoided by animals ( $\beta$  was negative for both variables), (ii) cracks made suitable roosts for bats in two models. Cavities used by bats were significantly located in main branches ( $n = 5$ ), and not in secondary branches and to some extent trunks

( $\chi^2 = 30.92$ ,  $d.f. = 2$ ,  $P < 0.001$ ). Bats did not occupy cavities in branches less than 15 cm in diameter.

The number of openings was greater in used than in unused cavities ( $1.46 \pm 0.61$  vs.  $1.16 \pm 0.46$ ; Mann-Whitney test:  $W = 9466.5$ ,  $P < 0.001$ ). Some models ( $n = 2-3$ ) retained additional variables such as the length of opening, which should not be too obstructed by development of a healing callus or by nesting nuthatch. On the contrary, bats selected cavities with an obstacle in the flight path (leaves or branches), especially if the obstacle is before the entrance. The inner diameter of the cavity was larger. The inner height above the entrance tended to be greater in used than in unused cavities ( $8.74 \pm 14.76$  cm vs.  $3.32 \pm 10.49$  cm;  $t = 3.56$ ,  $d.f. = 546$ ,  $P < 0.001$ ). Cracks and cavities with both upward and downward developments were more frequently used than other types of cavities ( $\chi^2 = 28.01$ ,  $d.f. = 7$ ,  $P < 0.001$ ). For five variables, the Wald statistic was zero, denoting that the regression coefficients were not significant.

#### *Effect of Potential Competitors*

Once potential competitors were included in the set of variables, logistic regressions predicted the

TABLE 2. Contribution of the variables to logistic regressions (10 models) predicting the use of tree cavities by bats in the Rambouillet forest (France), without and with potential competitors.  $\beta$  is the regression coefficient of each variable (positive values indicate that the variable contributes positively to the use of the cavity by bats). Wald is a statistic that calculates a value attributed to each regression coefficient in order to test the contribution of the corresponding variable

Variable	Without potential competitors			With potential competitors		
	Number of models	Mean $\beta$	Wald	Number of models	Mean $\beta$	Wald
Opening height	10	0.005	5.320	9	0.005	4.540
Condition of the wood	9	-0.443	13.206	9	-0.535	16.420
Peeling bark	9	-2.896	10.778	7	-3.129	8.667
Height above the entrance	7	0.178	16.171	7	0.151	6.463
Cavity in secondary branch	6	-1.759	12.043	8	-1.761	11.950
Cavity depth below the entrance	6	0.056	6.614	2	0.066	10.130
Cavity in main branch	5	1.881	8.669	5	1.633	7.832
Various recesses	5	-1.436	5.547	4	-1.788	5.471
Number of openings	5	1.371	12.029	3	1.589	6.775
Horizontal tube	4	-2.622	3.925	4	-2.929	3.806
Column with several openings	3	-22.495	0.0	3	-22.046	0.0
Cause of obstruction	3	-1.929	3.295	2	-2.759	4.167
Distance to obstacle in flight path	3	-0.163	9.352	4	-0.188	6.945
Large woodpecker hollow	2	-23.333	0.0	1	-23.919	0.0
Vertical upward and downward tube	2	11.258	2.241	7	5.239	4.106
Entrance on main branch	2	-2.125	7.710	1	-20.833	0.0
Crack	2	1.722	3.868	3	1.515	5.765
Obstacle in flight path	2	1.673	4.202	2	2.710	4.320
Entrance on trunk	2	-0.842	6.150	1	-1.039	5.288
Vertical downward tube	2	0.307	4.275	2	3.760	5.135
Length of opening	2	0.228	13.688	2	0.191	16.014
Inner diameter	2	0.073	6.799	4	0.059	8.617
Height above the entrance	2	0.049	3.788	3	0.104	4.104
Vertical upward tube	1	22.909	0.0	1	22.909	0.0
Rotten heart	1	-22.261	0.0	1	-22.563	0.0
Entrance facing east	1	-1.752	4.641	1	-1.972	5.613
Entrance obstruction	1	-0.957	4.405	4	1.860	5.208
Cavity in trunk	1	-0.726	5.374			
Gap under bark	1	22.641	0.0			
Outer diameter	1	-0.028	4.686			
Spider webs				7	-1.874	11.760
Hymenoptera				3	2.458	3.822
Humus				3	0.396	5.176
Bird				2	-2.667	4.493
Entrance facing south-west				1	-2.349	3.910
Medium woodpecker hollow				1	1.091	4.223
Presence of polypores				1	0.803	3.916

use ( $92.3\% \pm 4.3\%$ ) versus non use ( $81.8\% \pm 1.1\%$ ) of cavities better. The same five main variables contributed to more than half of the models (Table 2). Bats chose cavities with high opening ( $n = 9$  models), high above the ground ( $n = 7$ ), grooved in healthy wood ( $n = 9$ ), and avoided secondary branches ( $n = 8$ ) and peeling bark ( $n = 7$ ).

They also used vertical upward and downward tubes ( $n = 7$ ), whereas spider webs were incompatible with bat use ( $n = 7$ ). On the other hand, bats regularly used cavities with traces, even recent, of previous use by Hymenoptera (hornets, wasps or bees), and cavities lined with humus as the result of wood-decomposition by arthropods ( $n = 3$ ).

The main difference between the two sets of regression analyses refers to entrance obstruction ('cause of obstruction' and 'obstacle in flight path'). When there was potential competition with other tree-dwelling species, bats preferentially used cavities with an entrance which was obstructed ( $n = 4$ ).

#### Temperature

Although mean, maximum and minimum temperatures varied from one ten-day period to the next, mean temperatures inside and outside a cavity did not differ significantly ( $17.59 \pm 3.76^\circ\text{C}$  and  $17.85 \pm 4.07^\circ\text{C}$ , respectively;  $F = 0.05$ ,  $d.f. = 1$ ,

$P = 0.82$ ). The difference was significant for maximum and minimum temperatures ( $F = 312.4$ ,  $d.f. = 1$ ,  $P < 0.001$  and  $F = 266.6$ ,  $d.f. = 1$ ,  $P < 0.001$ , respectively). The highest temperature recorded was  $42.55^{\circ}\text{C}$  outside a cavity, and  $37.17^{\circ}\text{C}$  inside, whereas minimum temperatures reached the lowest temperature of  $5.55^{\circ}\text{C}$  inside a cavity (used by bats) versus  $5.70^{\circ}\text{C}$  outside.

Maximum temperatures were significantly different among sites ( $F = 13.8$ ,  $d.f. = 5$ ,  $P < 0.001$ )

and depending on expositions ( $F = 8.3$ ,  $d.f. = 7$ ,  $P < 0.001$ ), site ( $25.55 \pm 5.81^{\circ}\text{C}$ ), with sites 6 ( $25.41 \pm 5.21^{\circ}\text{C}$ ) and 1 ( $25.00 \pm 5.42^{\circ}\text{C}$ ) being hotter than sites 4 ( $21.52 \pm 4.25^{\circ}\text{C}$ ) and 2 ( $21.96 \pm 5.48^{\circ}\text{C}$ ). The hottest exposition was north ( $26.12 \pm 5.05^{\circ}\text{C}$ ) and the 'coldest' was east ( $20.96 \pm 5.05^{\circ}\text{C}$ ).

Finally, mean and maximum temperatures inside used and unused cavities (Fig. 2) were not significantly different (mean temperature  $17.58 \pm 3.93^{\circ}\text{C}$  vs.  $17.79 \pm 3.93^{\circ}\text{C}$ ;  $F = 0.01$ ,  $d.f. = 1$ ,  $P = 0.90$ ;

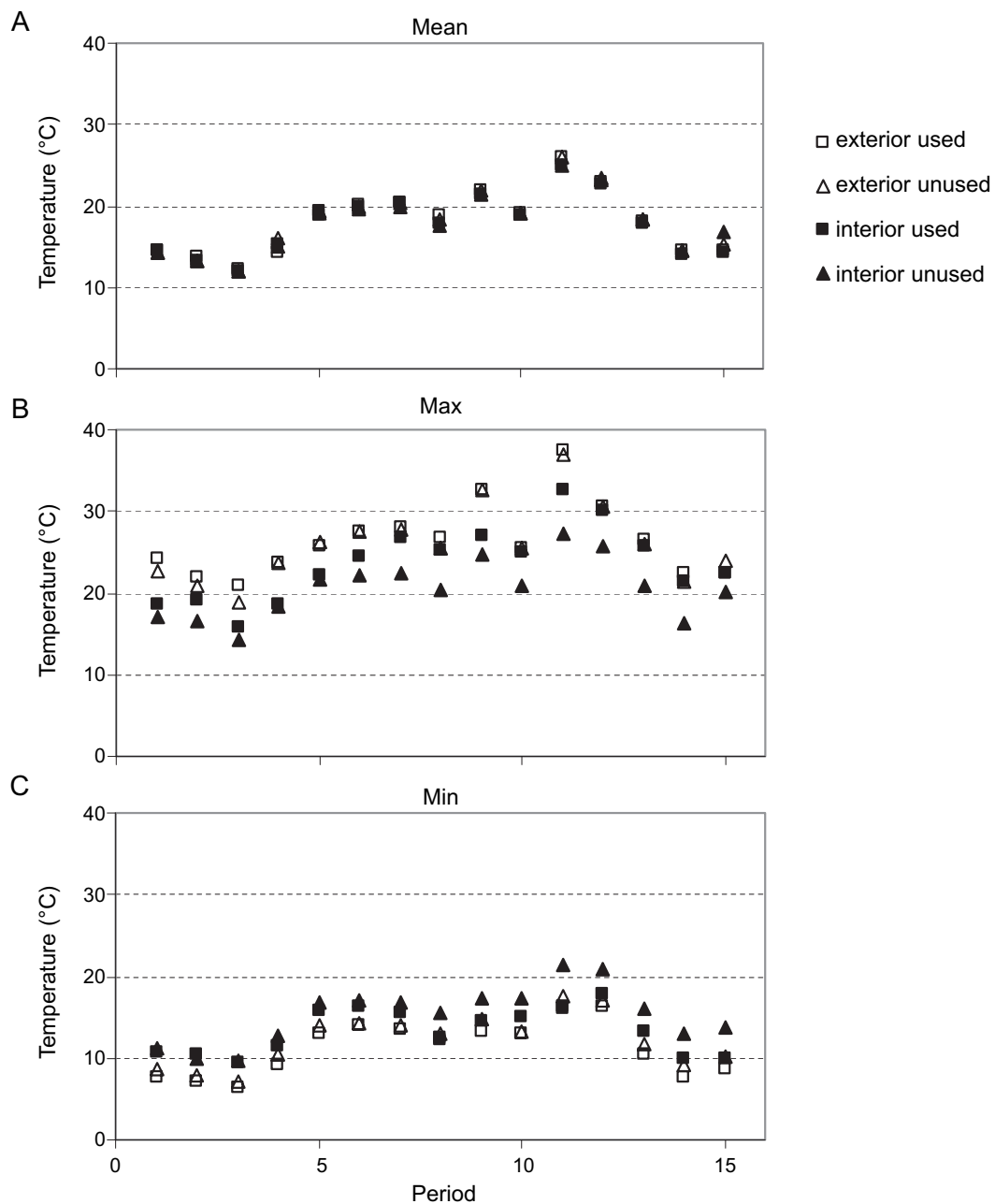


FIG. 2. Mean (A), maximum (B), and minimum (C) temperatures per 10-day periods inside and outside 30 cavities in trees of the Rambouillet forest (France); 20 were unused and 10 were temporarily used by bats. From period 1 = April 10 to 20 to period 15 = September 1 to 10

maximum  $23.32 \pm 5.66^{\circ}\text{C}$  vs.  $24.00 \pm 5.2^{\circ}\text{C}$ ;  $F = 0.00$ ,  $d.f. = 1$ ,  $P = 0.93$ ). Minimum temperatures were significantly higher in used than in unused cavities ( $13.30 \pm 3.77^{\circ}\text{C}$  vs.  $12.34 \pm 3.81^{\circ}\text{C}$ ;  $F = 312.4$ ,  $d.f. = 1$ ,  $P < 0.001$ ).

## DISCUSSION

### *Roost Typology*

Our results show that cracks, gaps under peeling bark and medium woodpecker hollows were the most abundant cavities in Rambouillet forest, and comparatively the most frequently used by bats. This is consistent with several autecological studies: cracks are known to be commonly selected by both *Plecotus auritus* and *Myotis nattereri* (Pénicaud, 2002) and woodpecker hollows by *Nyctalus noctula* (Ruczyński and Bogdanowicz, 2005) and *Myotis bechsteinii* (Kerth *et al.*, 2001a). Only a small proportion of cavities used by bats are linked to the decline of trees, in particular to peeling bark (3% used) and to developing decay (33% used), although several species seem associated with such roosts: *Nyctalus leisleri* (Ruczyński, 2004), *Barbastella barbastellus* (Russo *et al.*, 2004), *Myotis brandtii* (Sachanowicz and Ruczyński, 2001), *Myotis alcaethoe* (von Helvesen *et al.*, 2001) as well as *Pipistrellus* spp. (authors' personal observation). Some of these species, such as *N. leisleri* and *B. barbastellus*, are rare in Rambouillet forest (Tillon, 2007) where standing dead trees have been eliminated for several centuries. And even though management has changed in the last decade (Tillon, 2007), these bat species have not yet colonised the forest. Roost availability seems to be a limiting factor for some species, as it was already suggested by several authors (see Kalcounis-Rüppell *et al.*, 2005).

### *Roost Characteristics*

Based on our analysis bats seek a trade off between a great height above the ground, large internal dimensions of the cavity and an opening as high and narrow as possible. Some species, such as *Nyctalus* spp. (Ruczyński and Bogdanowicz, 2005) and *B. barbastellus* (Russo *et al.*, 2004) roost very high in trees. However, the higher the cavity is, the smaller the dimension of the host branch, as such branches deteriorate more quickly (Dajoz, 1998). Consequently, the cavities with a large upward and downward development and a long, narrow and high opening were rare but favoured by bats.

*Pipistrellus pipistrellus* was the only species roosting in dead trees, and under peeling bark. This design of the opening is commonly regarded as a strategy to reduce both predation and competition for cavities (Ruczyński and Bogdanowicz, 2005) or to find adequate microclimatic conditions (see Kalcounis-Rüppell *et al.*, 2005). Willis *et al.* (2006) and Kalcounis & Brigham (1998) even consider that bats choose lasting cavities that can be used repeatedly by the colony.

The use of cracks and woodpecker hollows high up in healthy trees is associated with a high density of branches or leaves in front of the entrance. So bats could benefit by some shelter from predators, wind or rain when emerging (Boonman, 2000). However, Mayle (1990) suggested that the flight path is better if clear of obstacles. This discrepancy can be explained by the morphology and the ecology of the species using the cavity. Most of the smaller species are able to fly in a cluttered environment, whereas some larger species such as noctules require relatively open air ways (Altringham and Fenton, 2003). Thus the latter should select cavities with more clearance in front of the entrance (Ruczyński and Bogdanowicz, 2005). Distance to obstacle in the flight path often came out with a negative coefficient in both sets of logistic regressions, and indeed small-sized and/or gleaning bats were more abundant at our study site than noctules (and serotines).

In our study, orientation of the entrance had little impact on cavity use, although entrances facing east or south-west seemed to be less favoured than others, even if openings facing the sun could contribute to raise the temperature inside the cavity and favour its use by bats (Kalcounis-Rüppell *et al.*, 2005). Ruczyński (2006) suggested that cavities exposed to sunlight high up in trees could provide a warm roost to both the young and the entire colony. This choice would help to minimise energy loss or to maintain a high metabolic rate (Ruedi, 1993) appropriate to social activity throughout the day. However, Ruczyński and Bogdanowicz (2005), and Sedgeley and O'Donnell (1999) also reported that orientation did not have a large effect on roost selection.

### *Potential Competition for Roosts*

Spider webs were repeatedly negatively correlated to bat use in the models. When present at the entrance of a cavity, spider webs are evidence that the cavity has not been recently used by bats

(Tidemann and Flavel, 1987). Moreover, we rarely found old guano in these cavities.

None of the visited cavities have been used by bats and birds in the same year, which could be a sign, underlined by two models, that some competition occurs. On the contrary, arthropod activity was frequently observed at the bottom of used cavities, possibly related to the bat guano and urine that favour insects (Neuweiler, 2000), including mites (Devetter, 2004), some of which are bat parasites.

Used cavities regularly contained recent remains of Hymenoptera nests (which usually disintegrate rapidly). Although bats probably do not share roosts with these aggressive insects, they may use the cavities in the same year. Bats may even benefit from the remains of nests, possibly for microclimatic characteristics, such as relative humidity, the atmospheric water being stored by the cellulose. Sedgely (2001) showed that the microclimate influences the use of cavities by *Chalinolobus tuberculatus*, while conversely the presence of bats may contribute to limit water loss by the host tree (Webb *et al.*, 1995). Alternatively *Vespa crabro* and bats could have similar requirements regarding their nesting/roosting sites in trees.

Entrance obstruction was selected in models with potential competitors. Indeed Ruczyński and Bogdanowicz (2005) showed that noctule bats select cavities with a narrower opening when predators, mainly *Martes martes*, were present. This had no effect on the presence of spiders, which can use small holes.

#### *Role of Temperature*

Temperature significantly differed among cavities. Lower temperatures were recorded for east-oriented cavities, possibly due to their short sun exposure. Surprisingly higher temperatures were recorded for north-oriented cavities, which could be explained by the thickness of wood between the cavity and the opposite south-oriented side of the branch.

Unlike the results of many studies (e.g., Entwistle *et al.*, 1997; Harbusch and Racey, 2006), mean and maximum temperatures did not differ between bat roosts and other cavities. This may be explained by the partial use of roosts over the 10-day periods of data collection due to the frequent roost switching of forest bat species (Willis and Brigham, 2004). Fitting the data loggers just below the entrance (whereas bats tend to prefer the upper parts of roosts) and pooling the data over the whole day could also bias the analysis. Ruczyński (2006)

reported that pregnant and lactating *N. noctula* and *N. leisleri* selected warmer cavities regarding mean and minimum night temperatures. Kerth *et al.* (2001a) did not find any significant differences in day-time temperature whereas night-time temperature seemed to be determinant for roost selection by *M. bechsteinii*. These results are nevertheless consistent with the significantly higher minimum temperature that we recorded. Given the position of the data loggers and the short occupancy of cavities by bats, we do not believe that their presence could change the roost temperature as suggested by Syme *et al.* (2001). Then, bats should select warmer cavities during the night only when energy loss is maximum, particularly for young (Speakman and Thomas, 2003), and could temporarily use colder cavities associated with periods of torpor (Willis, 2006).

#### CONCLUSION

In accordance with the autecology of the species inhabiting the Rambouillet forest, the most typical cavity used by bats in this Atlantic temperate lowland area consists of a medium woodpecker hollow or a crack located in a healthy part of tree. The cavity is high above the ground, has a narrow entrance and a large vertical development. Roosts are confined spaces that exclude competition with other taxa rather than cavities characterised by optimal microclimatic conditions. Given the number of bats liable to use tree cavities, the rarity of some species suggests that the number of available potential roosts may indeed restrain the presence of bats in the forest. Furthermore, the presence of cavities and their use by bats is doubtless linked to some specific characteristics of trees, such as foliage bearing, wood hardness or dendrometric features. In forests trees are not isolated, so their surroundings should also be investigated, such as the specifics of nearby trees, as well as presence of landscape features such as water bodies or forest tracks. Night roosts, which are only used for resting a couple of hours during the night, also deserve further research. For example, Ruedi (1993) showed that for *Myotis daubentonii*, such night resting sites can be critical at certain periods of the year or in case of sudden adverse weather conditions.

Our results suggest that forest managers should keep trees that are old enough to provide suitable cavities in healthy wood for most bat species, and should also keep decaying plots for maintaining the more specialised species (see Guldin *et al.*, 2007).

Foresters are presently requested to preserve dead trees to conserve the saproxylic biodiversity. Our results suggest that they also must conserve live trees with medium woodpecker hollows or cracks located in the healthy part of trees.

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# Tree selection by roosting bats in a European temperate lowland sub-Atlantic forest

**Abstract:** Trees are the main roosts for several European bat species but forestry practices are most often detrimental for them. After checking for the presence or absence of bats in trees, we collected a number of variables to describe trees within a lowland sub-Atlantic oak-dominated forest. We modelled the usage of the trees by bats according to the main characteristics of trees (11 quantitative and 13 qualitative variables) with a logistical regression analysis. Our results show that the number of cavities in the tree is the main variable that induces the occupancy by bats. There is a “typical” lowland tree preferred by bats which is a healthy oak tree of large diameter. We finally provide some guidance for woodland managers to maintain bat roosts, including maintaining some trees of large diameter, protecting small areas of old trees with cavities).

**Keywords:** Chiroptera; oak; predictive analysis; tree roost; woodland management.

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## Introduction

During their diurnal rest, bats mainly depend on the availability of roosts to avoid predators and/or to enjoy optimal climatic conditions (Kunz and Fenton 2003). The number of roosts used by woodland bat species throughout the season is generally high, even if bats are faithful to a roosting area (Boonman 2000, Kerth et al. 2001b, Ruczyński and Bogdanowicz 2005). The first condition for the presence of bats in a tree is obviously the availability

of suitable cavities (Entwistle et al. 1997, Kunz and Fenton 2003, Ruczyński and Bogdanowicz 2005).

All tree species be they broad-leaved or conifers can be used by bats (Kalcounis and Brigham 1998, Chung-MacCoubrey 2003, Russo et al. 2004, Pénicaud 2006), but a recent summary on this topic in North America reports that bats have a tendency for selecting relatively small trees with a large diameter, a relatively sparse crown and a large number of potential cavities (Kalcounis-Rüppell et al. 2005). Some species such as *Lasiurus borealis* (Müller, 1776) however prefer dominant or co-dominant trees with a crown thicker than most trees (Limpert et al. 2007). The understorey is then very sparse. As a rule cavities are associated with a large diameter, a great height, a high longevity, the dieback of a tree and its natural degradation (Taylor and Savva 1988, Weller and Zabel 2001, Fellers and Pierson 2002). Biotic factors can also contribute to hollow these cavities such as fungi, saproxylic insects or woodpeckers (Dajoz 1998, Hatsch et al. 1999, Blondel 2003). In their study on roosts used by *Eptesicus fuscus* (Beauvois, 1796), *Lasionycteris noctivagans* (Le Conte, 1831), *Myotis evotis* (H. Allen, 1964) and *Myotis volans* (H. Allen, 1866) in conifer woodlands, Vonhof and Barclay (1996) show that only three variables were significant, bats preferring tall trees, with sparse leaf coverage and relatively close to other trees with cavities. In Europe, *Nyctalus noctula* (Schreber, 1774) were most often found in live trees (Ruczyński and Bogdanowicz 2005), *Barbastella barbastellus* (Schreber, 1774) prefers dead trees (Russo et al. 2004, Hillen et al. 2010, Russo et al. 2010) and *N. leisleri* (Kuhl, 1817) occupy both types of trees (Ruczyński and Bogdanowicz 2005). However several authors suggest that live trees are more favourable to host breeding colonies (Kalcounis and Brigham 1998, Kerth and König 1999, Willis et al. 2006). This was reported for broad-leaved trees whereas dead trees were preferred in conifers (Zielinski and Gellman 1999, Chung-MacCoubrey 2003, Baker and Lacki 2006). Most studies are based on quantitative variables, mainly dendrometric measurements (diameter and height of trees for instance), few of them include tree geometry. However the size and shape of the crown plays an important role in the development of trees and associated micro-habitats (Hallé 1999). Qualitative variables seem more difficult to record and analyse,

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**Table 1:** Main characteristics of the six plots sampled in the Forest of Rambouillet (France) for the study of tree selection by roosting bats.

	Plot A	Plot B	Plot C	Plot D	Plot E	Plot F
Type of forest	High forest	Coppice-with-standards	Coppice-with-standards cleared in places	Coppice-with-standards cleared	Coppice-with-standards being converted to high forest	Coppice-with-standards cleared in places
Soil quality	Rich	Rich	Poor	Rich	Poor	Poor
Dominant species	<i>Quercus petraea</i>	<i>Q. petraea</i> , <i>Fagus sylvatica</i>	<i>Q. petraea</i> , <i>F. sylvatica</i>	<i>Q. petraea</i>	<i>Q. petraea</i>	<i>Q. petraea</i> , <i>Populus tremula</i> , <i>Carpinus betulus</i>
Forestry management objective	Biodiversity reserve	Production	Landscape preservation	Production	Production?	Biodiversity reserve
Presence of ponds	Yes	No	Yes	No	No	Yes
Size of plot (in ha)	4.7	4.8	9.7	10.0	6.0	4.7

particularly for bats which move in a three-dimensional space and do not use predominantly visual clues.

The major difficulty when studying bats in woodlands remains the finding of roosts. These animals are very inconspicuous and their discovery can be hazardous (Willis et al. 2006), due to frequent changes of roost in quite large areas, despite a high fidelity to roosting zones. Indeed, surveys can not rely on data solely gathered from the ground but need to visit the cavities for checking the presence of animals or signs (droppings, urine, carcasses). Most studies on bats in forests were restricted to the description of trees used by some radiotracked individuals (Vonhof and Barclay 1996, Crampton and Barclay 1998, Menzel et al. 2002, Russo et al. 2004, Ruczyński and Bogdanowicz 2005), and did not consider the whole roosting opportunities of the forest.

To provide woodland managers with guidance to maintain bat populations in temperate lowland sub-Atlantic forests we studied the roosting potentiality of a large forest complex of 22,000 ha. We surveyed all trees with cavities to predict the presence or absence of bat colonies, whatever species they are. We then identified the main characteristics of trees, used by bats or not, that could be easily evaluated from the ground by woodland managers.

## Materials and methods

### Study area

The Forest of Rambouillet is located 70 km South-West of Paris (France). This is a lowland sub-Atlantic broadleaf wood, dominated by oak trees *Quercus petraea* et *Q. robur*, with secondary species such as common beech *Fagus*

*sylvatica*, aspen *Populus tremula*, birch *Betula sp.*, hornbeam *Carpinus betulus*, wild cherry *Prunus avium*, service *Sorbus torminalis*, ash *Fraxinus excelsior*, apple *Malus sylvestris* or sweet chestnut *Castanea sativa*. Conifers, including Scots pine *Pinus sylvestris*, occurred on 20% of the woodland area. A total of 19 bat species were recorded by Tillon 2007, including tree-dwelling species such as *Myotis bechsteinii* (Kuhl, 1817), *M. daubentonii* (Kuhl, 1817), *M. mystacinus* (Kuhl, 1817), *M. nattereri* (Kuhl, 1817), *Nyctalus noctula*, *N. leisleri*, *Eptesicus serotinus* (Schreber, 1774), *Pipistrellus pipistrellus* (Schreber, 1774), *Plecotus auritus* (Linnaeus, 1778) and *Barbastella barbastellus*.

As it was not possible to find all cavities (Tillon and Aulagnier 2014) used by bats, six plots of 4.5–10 ha including at least 30 trees with cavities were sampled from April to September 2003. These plots, representative of the various management operations of the forest, were dominated by oak trees, or by a mix of common beech and oak trees (Table 1).

### Searching for trees with cavities

In the six plots we surveyed and described all trees at least 7 cm in diameter, and visited each tree with at least one cavity, using a ladder for cavities up to 5 m high, or by climbing to the highest cavities (27 m). The presence of bats in trees was assessed either by visual observation or by signs (droppings, urine and carcasses) in the cavities (Tillon and Aulagnier 2014).

### Tree description

Trees are usually described by the tree species, the diameter at human breast height, the height of the tree, its

social position (dominant or dominated), its inclination, the number of branches, the presence of signs of disease or decay undermining the tree, or its stage of decay (Taylor and Savva 1988, Kalcounis and Brigham 1998, Sedgeley and O'Donnell 1999a,b, Zielinski and Gellman 1999, Menzel et al. 2002). The location of the tree within the forest stand was also taken into account (Vonhof and Barclay 1996). Vonhof and Barclay (1996) measured the percentage of bark remaining on conifers, and Crampton and Barclay (1998) took the same measure on broad-leaved trees. Betts (1998) recorded the crown cover for each tree with cavities. The health of the tree was also important (Sedgeley and O'Donnell 1999a,b, Waldien et al. 2000).

Therefore each tree was described by 24 variables, including the status and shape of the tree (species, social status, quality of wood, a variable used to estimate the value of a logging area), its structure (heights, diameter, etc.) and health (foliage, vitality, malformations or signs of weakness such as loose bark, flows, malformations of trunk, spins, insect holes, fungi). The quality of wood is routinely recorded by forest managers and is therefore interesting when proposing conservation management. It also provides information on the health of the individual tree and even on its ability to heal after being wounded.

Eleven quantitative variables were recorded: (1) total height (m); (2) height of the first branches (m); (3) height of the base of the crown (m); (4) height of the log (part of the tree that can be exploited, in m); (5) diameter (cm) at 1.30 m height; (6) 'plank height' (term of forestry used for trees with straight fibres, more or less tight, on a trunk without defects, which reflects a very high technical quality of wood, therefore of great economic value); (7) mean longest distance between the extremity of foliage and the trunk in the four directions that is called radius of the crown (N, E, S, W, in m); (8) crown volume (calculated in m<sup>3</sup> using the mean distance of the extremity of foliage to the trunk and the height of crown); (9) height of the break (m) in the case of broken tree; (10) number of areas of peeling bark; (11) number of cavities.

The thirteen qualitative variables were recorded as follows: (1) tree species (oak, beech, aspen, birch, other broad-leaved trees, pine); (2) social status (dominant, co-dominant, dominated or co-dominated); (3) quality of wood (from a very poor quality to a high quality); (4) shape of the top (no top, sparse top, pyramidal top, ovoid top, erect top, bulging top); (5) shape of the crown (compressed, normal, spread out, very broad); (6) stature of the tree (standing, bent, hung-up, candle-like, on the ground);

(7) vitality of the tree (from 1 - healthy, to 5 - dead with missing bark and heart altered); (8) status of the foliage (from 1 - almost absent, to 3 - dense); (9) flows of mucilage, sap, gum, black marks on the trunk (absent, lower trunk, middle of the trunk, upper trunk, limb, top log or part of the tree above the first branches); (10) malformations of trunk (absent, lower trunk, middle of the trunk, upper trunk, limb, top log or part of the tree above the first branches); (11) spins (important for the mechanical characteristics of the wood, absence, presence) and position (absence, presence); (12) insect holes (absence, presence); (13) fungi (absence, presence).

## Data analysis

The relationship between tree diameter and number of cavities was studied with a Spearman test. The relationship between tree species and number of cavities, and between vitality of the tree and number of cavities, were studied by Kruskal-Wallis tests.

To predict the presence and absence of bats in a cavity, we then ran a step-by-step logistic regression using SPSS software (version 9.0, Norusis 1999). This method is most suited to situations related to the presence or absence of a feature (here the absence or presence of bats), for a large number of qualitative and / or quantitative variables regardless of their distributions (Keating and Cherry 2004).

Owing to the low number of trees used by bats (39) compared to unoccupied trees (226), we investigated the best allocation between the two options of the variable to make the prediction. The proportion 1/3 of occupied trees for 2/3 of unoccupied trees with cavities appeared the most effective for a balanced prediction. Fifteen samples were extracted from the dataset, including all 39 occupied trees and a random set of 80 unoccupied trees with cavities. We then calculated an average rate of prediction for the regression coefficient B for each variable (which gives a relative contribution of the variable to the prediction, a positive value means that the variable contributes positively to the presence of bats), and for the Wald statistic (which gives a value for each coefficient, and allows to test the contribution of each variable; following a  $\chi^2$  distribution for large samples).

The logistic regression was performed in two steps, (i) with all the descriptive variables, (ii) then by removing the variable "number of cavities", which is an integrative variable depending on the structure and stature of the tree. The distribution of trees for the relevant variables identified by the regressions was analyzed using Student's

t-tests and  $\chi^2$ -tests according to their nature (qualitative vs. quantitative).

## Results

### Trees with cavities

Out of the 3942 surveyed trees, 265 had at least one cavity (Table 2). Oak (mainly *Quercus petraea*, more rarely, *Q. robur*) was the species with the greatest number of cavities (77.0% of trees with cavities). We found cavities in birch (9.4%), hornbeam (7.9%), beech (2.3%), aspen (0.8%), pine (0.8%) and other trees (as apple, chestnut, wild cherry, service: 1.8%).

The minimum diameter of a tree with a cavity that can accommodate bats was 12 cm. Above this value, the number of cavities increased with the diameter of the tree (Figure 1). Beyond 65 cm in diameter, the number of trees decreased dramatically and the number of cavities became independent of the diameter. This is a sign of the significant exploitation of large trees for timber production, whether cavities are present or not. Nevertheless the Spearman test was highly significant ( $\rho_s=0.023$ ,  $Z_{rs}=6.28$ ,  $p<0.001$ ).

The relationship between tree species and number of cavities was not significant ( $H=4.48$ ,  $df=6$ ,  $p=0.611$ ), the cavities did not develop in particular species. Finally, the relationship between the number of cavities and the health of trees was close to the significance level ( $H=8.88$ ,  $df=4$ ,  $p=0.064$ ). The cavities were formed or were being hollowed in healthy trees, but more often in decaying trees or in dead trees.

### Bats in trees with cavities

The use of cavities by bats was identified either by presence of animals (in 5.7% of cases) or mainly by signs of presence in 97.5% of cases.

### The influence of the number of cavities

The first set of logistic regressions produced very high prediction rates, with 94.4% ( $\pm 2.6\%$ ) for occupied trees and 96.7% ( $\pm 3.3\%$ ) for non-occupied trees.

The number of cavities appeared to be the predominant variable in the selection of trees by bats (variable relevant in 15 models, Wald statistic=9.859, Table 3). There was a positive correlation between the number of cavities and the chance that the tree hosted bats ( $B=2.530$  and  $t$ -test=7.9,  $df=38$ ,  $p<0.001$ ).

No other variable was relevant in more than half of the 15 models, it was therefore difficult to interpret this result further.

### Influence of other variables

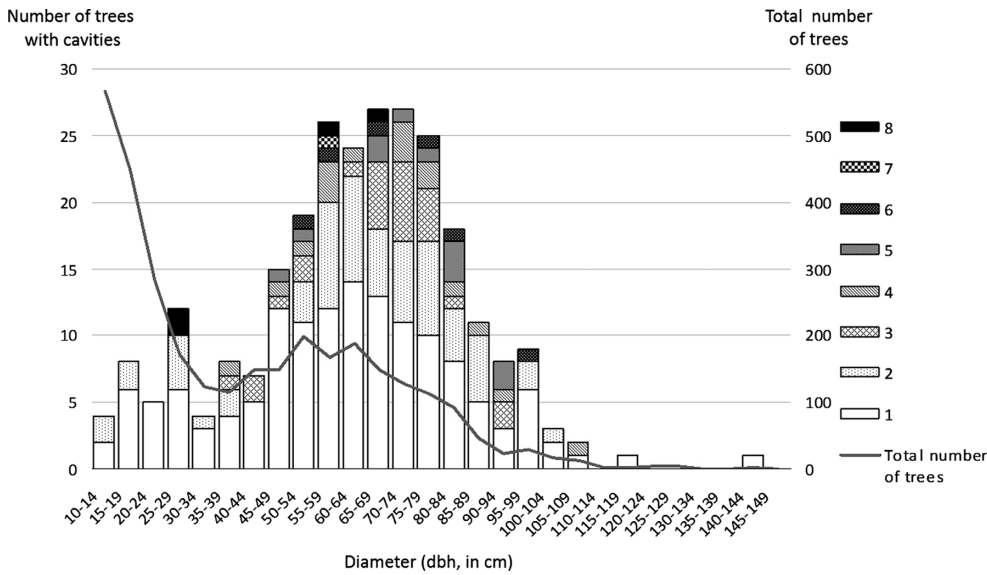
The second set of logistic regressions (without the variable “number of cavities”) produced medium to low prediction rates, with 88.7% ( $\pm 5.5\%$ ) for occupied trees and only 66.0% ( $\pm 15.7\%$ ) for non-occupied trees. Seven variables were relevant in more than half of the models, four were already selected by the first set of regressions. Among these variables, some species and the diameter of the tree were variables integrated by the number of cavities.

“Species” was a variable highly selected by the models ( $\chi^2=24,355$ ,  $df=3$ ,  $p<0.001$ , see Figure 2). “Oak” was the species most likely to host bats (13 models;  $B=0.842$ ). On the contrary, birch (15 models;  $B=-2.357$ ) was clearly avoided by bats, more so than hornbeam (4 models,  $B=-1.576$ ) or beech (model 1,  $B=-1.946$ ). Indeed, 89.7% of cavities selected by bats were in oaks, which represented 17.0% of all oaks with cavities. Only two hornbeams and one beech were also occupied out of, respectively, 21 and 6 cavity trees for these species.

Among the dendrometric variables “diameter” was selected (10 models;  $B=0.023$ , with high significance:  $t=7.54$ ,  $df=39$ ,  $p<0.001$ ), much more than the “height of the log” (3 models;  $B=0.134$ , with  $t=5.500$ ,  $df=40$ ,  $p<0.001$ ).

**Table 2:** Number of trees with and without cavities for the main tree species recorded in six plots of the Forest of Rambouillet (France).

	Birch	Hornbeam	Oak	Beech	Aspen	Other broad-leaved trees	Pine	Total
With cavity	25 2.6%	21 2.9%	204 14.2%	6 1.0%	2 2.2%	5 6.4%	2 4.3%	265
Without cavity	953 97.4%	706 97.1%	1235 85.8%	574 99.0%	91 97.8%	73 93.6%	45 95.7%	3677
Total	978	727	1439	580	93	78	47	3942

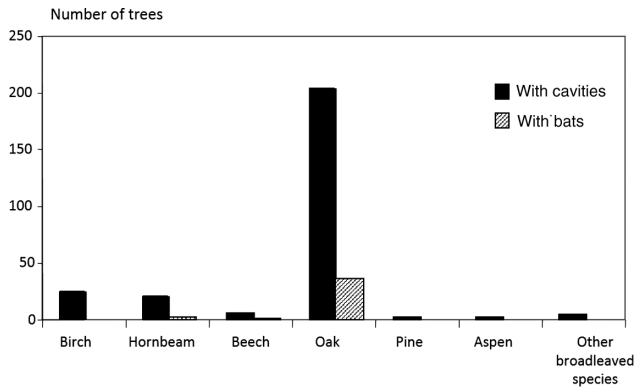


**Figure 1:** Total number of cavities per tree (in histograms, 1–8 cavities) and total number of trees (the grey line) for each class of diameter (5 cm increment) in six plots of the Forest of Rambouillet (France).

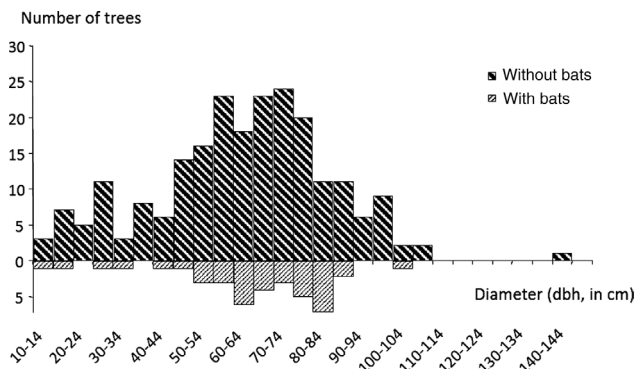
**Table 3:** Results of 15 logistic regressions for predicting the presence and absence of bats in trees with cavities in six plots of the Forest of Rambouillet (France), with and without the number of cavities within the descriptive variables.

Variables	With the number of cavities			Without the number of cavities		
	Total number of occurrence	B mean	Wald	Total number of occurrence	B mean	Wald
Birch				<b>15</b>	<b>-2.357</b>	<b>4.94</b>
Oak	2	4.344	8.782	<b>13</b>	<b>0.842</b>	<b>6.397</b>
Shape of the top	5	-6.285	7.968	<b>12</b>	<b>-0.67</b>	<b>8.043</b>
Fungi	1	-1.17	7.812	<b>11</b>	<b>8.883</b>	<b>0</b>
Diameter				<b>10</b>	<b>0.023</b>	<b>7.127</b>
Status of the foliage	7	6.252	1.728	<b>8</b>	<b>-0.901</b>	<b>10.875</b>
Coppice				<b>8</b>	<b>-21.679</b>	<b>0</b>
Spins				4	20.022	0
Hornbeam				4	-1.576	4.603
Height of the log				3	0.134	7.768
Social status	2	-0.826	14.49	2	-0.499	8.859
Crown volume	2	-0.001	4.449	2	0.001	6.608
Shape of the crown	1	-3.299	10.719	2	-0.948	5.177
Vitality of the tree	1	-1.656	19.09	2	0.775	5.238
Aspen				2	-22.578	0
Height of the first branches				2	-0.419	3.788
Status of foliage	4	-14.14	10.915	1	-0.36	6.952
Position of Malformations of trunk	2	1.953	3.333	1	0.228	5.552
Beech				1	-1.946	3.313
Plank height				1	0.756	2.783
Stature of the tree				1	0.581	6.402
Quality of wood				1	0.569	4.853
Radius of the crown				1	0.423	4.84
Total height				1	-0.206	11.662
Number of cavities	<b>15</b>	<b>2.53</b>	<b>9.859</b>			
Insect holes	2	-1.701	2.184			
Other broadleaves	1	-21.414	0			
Flows	1	-54.808	0			

B is the regression coefficient of each variable (positive values mean that the variable contributes positively to the presence of bats, and corresponds to a Wald statistic providing a value to test the contribution of each variable). Bold types emphasize variables which contribute to more than half models either with or without the number of cavities.



**Figure 2:** Number of trees with cavities (but without bats) and trees with cavities occupied by bats for the main tree species recorded in six plots of the Forest of Rambouillet (France).



**Figure 3:** Number of trees with cavities for each class of diameter in six plots of the Forest of Rambouillet (France): unoccupied by bats and occupied by bats.

and “plank height” (1 model,  $B=0.756$ ) which had a low significance ( $t=1.35$ ,  $df=38$ ,  $p=0.093$ ). Bats occupied trees with cavities from the smallest diameter to the largest (Figure 3). It turns out that the trees selected by bats did not have the best “quality of wood” (1 model,  $B=0.569$ ), even though the significance of this variable was low ( $\chi^2=3.452$ ,  $df=1$ ,  $p=0.063$ ). Selected trees often had spins on their trunk (a sign of deformation of the wood, sometimes becoming cracks) (4 models;  $B=20.022$ ), meaning that bats did not prefer trees with high commercial value.

The height of the first branches was also relevant (2 models;  $B=-0.419$ ), bats selecting trees with branches as low as possible. Although this variable was not significant ( $t=0.31$ ,  $df=40$ ,  $p=0.380$ ), this supports the previous statement concerning the commercial value of occupied trees, as low branches greatly reduce the quality of log.

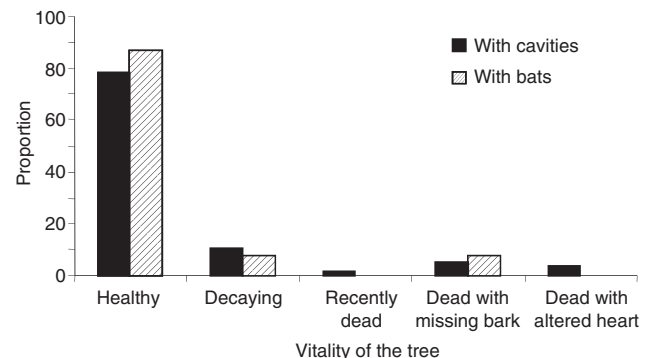
Some variables related to the shape or status of the tree were significant, such as the “shape of the top” (12 models;  $B=-0.670$ ) with more significance when

it is sparse ( $\chi^2=8.744$ ,  $df=3$ ,  $p=0.033$ ), social status (2 models;  $B=-0.499$ ) with a preference for dominant trees ( $\chi^2=8.927$ ,  $d=2$ ,  $p=0.012$ ), the “shape of the crown” (2 models;  $B=-0.948$  with a very broad crown,  $\chi^2=17.251$ ,  $df=3$ ,  $p=0.002$ ) and the position of malformations of trunk (1 model,  $B=0.228$ ) which also pointed downwards in trees selected by bats ( $\chi^2=7.891$ ,  $df=3$ ,  $p=0.048$ ). The trees primarily selected by bats belonged to the dominant stratum, but were not necessarily the tallest in the forest stand (total height: 1 model,  $B=-0.206$ ,  $t=3.13$ ,  $df=39$ ,  $p=0.002$ ) with foliage and branches rather high in the tree, producing an inverted conical crown and a top with a regular shape.

“Vitality of the tree” was a criterion for selection by bats (2 models,  $B=0.775$ ), with a preference for healthy trees ( $\chi^2=9.526$ ,  $df=2$ ,  $p=0.009$ ). Variables that indicate decay of trees or appearance of cavities, such as “insect holes”, as well as “flows” (mainly sap) and “fungi” which are characteristics of fungal attack (11 models but  $Wald=0$ ), lessened the role of the “vitality of the tree” to explain the selection of trees by bats. Figure 4 shows that bats could roost in dead or dying trees with cortical damage, but they mostly chose healthy trees. The trees showing signs of weakness had loose bark, and were exclusively used by *Pipistrellus pipistrellus*. This species alone could influence the models towards a type of tree different to those usually selected by all the other bat species of the forest.

## Discussion

Some authors (Sedgeley and O’Donnell 1999a, Limpert et al. 2007) find it difficult to interpret the predictive



**Figure 4:** Vitality of the trees with cavities ( $n=265$ ) and the trees occupied by bats ( $n=39$ ) in six plots of the Forest of Rambouillet (France) expressed as the proportion of the total number of trees of each category.

variables of the selection of a tree or a cavity by bats, mainly because of the difficulty of assessing the actual availability in potential roosting cavities for the species present. However, the “number of cavities” dominated over all other descriptive variables in our study and so should be considered as much as possible. Similarly, Willis et al. (2006) reported that the number of cavities in a tree and its diameter explain the selection by *Eptesicus fuscus*. The meta-analysis from North American studies in conifer forests (Kalcounis-Rüppell et al. 2005) also showed a positive effect of the density of cavities on the selection of a tree. In addition, the selected trees were mostly small, with a large diameter and fairly sparse foliage.

Some studies show that the number of cavities generally increases with the diameter of tree (Sedgeley and O'Donnell 1999a, Kunz and Lumsden 2003, Kalcounis-Rüppell et al. 2005, Ruczyński and Bogdanowicz 2005), and that bats use mostly large diameter trees. In our study this relationship is not obvious and bats also occupied small trees. The minimum diameter of a tree drilled by a woodpecker with cavities potentially used by bats was 12 cm, and this was 14 cm for cavities occupied by bats, a value already recorded by Martin and Eadie (1999), a bit less than the 18 cm reported by Pénicaud (2006). The presence and number of cavities also depend on the resources available to each tree. Indeed stress factors, that we did not study (soil characteristics, tree density, management activities, etc), may contribute to the development of cavities whatever the diameter of the tree (Hallé pers. comm.), especially if other variables such as vitality or shape of the foliage are involved.

The species mainly used by bats in our forest was oak *Quercus petraea*, which is the species that is largely dominant in the area, although other tree species hosted favourable cavities. This dominance of one tree species could generate this use. Similarly, Russo et al. (2004) highlighted a selection of beech by *B. barbastellus* in Italian forests largely dominated by this species. This preference of bats for oak trees could depend on the foliage, which is loose in the crown, and becomes looser with age. The other tree species which were occupied by bats, hornbeam and beech, have thicker foliage and a larger number of branches, which cut out light to the cavity. Bats may actually select trees for the number of cavities and also for the sun radiation which can potentially warm the trunk or the part of the tree hosting the roost, as reported by Vonhof and Barclay (1996), Crampton and Barclay (1998) or Ruczyński (2006). However, this remains an hypothesis as bats may also need a clearing in front of the roost, sufficient to allow the flight of the individuals of the colony, as Kerth et al. (2001a) recorded for *Myotis bechsteinii*.

On the contrary they could be more exposed to predators than in cluttered habitats (Russo et al. 2007). Few studies dealing with roosting behaviour considered the accessibility of cavities by tree-dwelling bats. Nevertheless, echolocation induces constraints that are magnified in cluttered environments, where bats use low intensity calls and can not distinguish very long distance barriers. They usually commute along wood-edges and clearings (both vertical and horizontal) and enter the foliage mainly for foraging. Trees selected for roosting offer large empty space that allows an easy access to the cavity, while offering landmark and potential protection against predators and bad weather conditions (Barclay and Kurta 2007). Moreover, the presence of foliage could be a good indicator of the sustainability of the cavity, as a healthy tree should stand up longer than a dead tree, which appears more favourable to breeding colonies (Kalcounis and Brigham 1998, Kerth and König 1999, Willis et al. 2006). Live oak trees with large diameters and sparse foliage offer the most suitable conditions for quick and safe emergence and return into the roost, and sunshine warming suitable for growth of young.

Finally, an original result was that roost trees had a lower quality of wood than unoccupied trees. Therefore it should be easier to convince forest managers to preserve them for bat conservation. Maintaining bat roosting trees might be acceptable within forestry management when timber production is the main objective.

## Conclusion

Our study of trees selected by bats in a European sub-Atlantic lowland oak-dominated forest showed that these are primarily oak trees of large diameter which can offer a large number of cavities, and potential roosts, a result that is highly consistent with the literature. The number of cavities in the surrounding trees could also be relevant as most tree-dwelling bats usually use a large set of roosts throughout the year (Kerth et al. 2001a, Kalcounis-Rüppell et al. 2005, Barclay and Kurta 2007) and even tree selection changes along the breeding season (Ruczyński and Bogdanowicz 2008). However, in our forest the distance between trees with cavities was similar to the distance to random trees (Tillon 2007). Bats also preferred live trees on which the foliage becomes looser with age, probably in response to a trade-off among accessibility, predation risk and microclimatic conditions. Canopy openness was also a factor identified in the meta-analysis reported by Kalcounis-Rüppell et al. (2005). Finally, most of roost trees belonged to the dominant species, but had cavities,

malformations of trunk, spines and other defects that reduce their economical value.

Trees of large diameter are usually cut down by forest managers for wood production. A first bat-friendly forestry practice should be to maintain some trees of large diameter, and lower wood quality, in order to provide bats with extent or future suitable cavities. In production plots these trees should act as stepping stones for breeding colonies when they move between roosts (Hayes and Loeb 2007, Wigley et al. 2007, Russo et al. 2010). A second practice should be to protect small areas of old trees with cavities, as the number of roosting sites is considered to be a limiting factor (Barclay and Kurta 2007, Guldin et al. 2007, Wigley et al. 2007, Russo et al. 2010). These reserves designated on the number of trees with cavities rather than on the species richness would be easier to identify for forest managers.

These are general guidance that applies to most tree-dwelling bat species. Our study did not aim to investigate specific bat selection of roosts and reaches a limit, as the roosting behaviour in trees of each species is different (e.g., Menzel et al. 2002, Weller 2007, Wigley et al. 2007). Improving this guidance in terms of bat conservation in highly harvested forests requires further investigations of the roosting behaviour of at least the more sensitive species.

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